

THE AMPHIPOD SUPERFAMILY PHOXOCEPHALOIDEA ON THE PACIFIC COAST OF NORTH AMERICA. FAMILY PHOXOCEPHALIDAE. PART II. SUBFAMILIES PONTHARPINIINAE, PARHARPINIINAE, BROLGINAE, PHOXOCEPHALINAE, AND HARPINIINAE. SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

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ABSTRACT

The systematics and distributional ecology of component members of phoxocephalidean amphipod subfamilies Parharpiniinae, Pontharpiniinae, Brologinae, Phoxocephalinae, and Harpiniinae in coastal waters of the Pacific coast of North America, from the Bering Sea to northern California, are analyzed. Of the 22 regional species here recorded, the following 11 species (50%) are new to science: Pontharpiniinae: *Mandibulophoxus mayi*, new species; *M. alaskensis*, new species; Brologinae: *Paraphoxus rugosus* new species, *P. pacificus*, new species, *P. communis*, new species, *P. gracilis*, new species, and *P. similis*, new species; Phoxocephalinae: *Parametaphoxus quaylei*, new species; Harpiniinae: *Pseudharpinia inexpectata*, new species; *Heterophoxus conlanae*, new species, and *H. ellisi*, new species.

The following taxon from outside the study region is also newly described: *Griffithsius*, new genus (South Africa). The following species are identified but not named: *Eyakia* species 1 (California), *Eyakia* species 2 (Alaska); *Parametaphoxus* species 1 (Japan), and *Heterophoxus* species 1 (California). The following taxa are newly recorded from the study region: *Mandibulophoxus gilesi* Barnard, 1957; *Eyakia robusta* (Holmes, 1908); *Harpiniopsis gurjanovae* (Bulycheva, 1936); *H. fulgens* (Barnard, 1960); *Paraphoxus simplex* Gurjanova, 1938; and *Cephalophoxoides homilis* (Barnard, 1960). The following species are re-recorded, redescribed and refigured on the basis of regional material: *Eobrologus chumashi* Barnard & Barnard, 1981; *Metaphoxus frequens* Barnard, 1960; *Heterophoxus affinis* (Holmes, 1908); and *Harpiniopsis fulgens* (Barnard, 1960). The copulatory apparatus of the male peraeopod 7 was found to be remarkably diverse in the present material, and proved helpful in clarifying taxonomic relationships.

Biogeographically, the subfamilies Parharpiniinae and Pontharpiniinae, dominant along temperate-tropical Indo-Pacific and antipodean shores, appear to be relict along northeastern Pacific shores. The Brologinae, common in protected coastal shallows of the northern and southern hemispheres, the Phoxocephalinae, world-wide mainly in deeper shelf waters, and the Harpiniinae, dominant on finer sediments and in deeper waters of the northern hemisphere, are well represented in the present study region. The Coxophoxinae and Joubinellinae, known from deep waters of adjacent regions, probably occur here also but were not identified.

Within the present study region, the total number of species of these five subfamilies combined is slightly less than that of the single regional subfamily Metharpiniinae (Jarrett and Bousfield, 1994). The present species were also taken less abundantly at stations with sandy sedimentary bottoms. Such bias may reflect their overall preference for finer, softer sediments, at greater depths, habitats that were not extensively sampled in present surveys. Only a few species of these subfamilies, notably within the primitive sand-burrowing Pontharpiniinae, occur commonly intertidally.

INTRODUCTION

Members of the gammaridean amphipod family Phoxocephalidae are sediment-burrowing crustaceans of distinctive morphology, life style, and reproductive behaviour. They are world-wide in distribution, and are abundantly represented on the Pacific coast of North America, from Alaska to California. In a previous systematic account of the large, mainly shallow-water subfamily Metharpiniinae in this region, Jarrett and Bousfield (1994) treated 29 species in 5 genera. With respect to seven other subfamilies (of Barnard and Drummond, 1978) recorded from (or probably occurring on) the North American Pacific coast, previous

records of 20 component species have been summarized variously by Austin (1985), (Cadien, 1991), and Barnard & Karaman (1991). These include the following (subfamily of this study in parentheses): *Mandibulophoxus gilesi* Barnard, 1957 (Pontharpiniinae); *Eyakia robusta* (Holmes, 1908) and *E. calcarata* (Gurjanova, 1938) (Parharpiniinae); *Eobrologus chumashi* Barnard & Barnard, 1981, *E. pontarpinioides* (Gurjanova, 1953), and *Paraphoxus oculatus* Sars, 1895 (Brologinae); *Cephalophoxoides homilis* (J. L. Barnard, 1960), *Metaphoxus frequens* (J. L. Barnard, 1960), and *Parametaphoxus fultoni* (Scott, 1890) (Phoxocephalinae); *Heterophoxus oculatus* (Holmes, 1908), *Heterophoxus affinis* (Holmes, 1908), *Harpinia crenulata* Boeck, 1871, *Harpin-*

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iopsis emeryi Barnard, 1960, *H. fulgens* Barnard, 1960, *H. galera* Barnard, 1960, *H. naiada*, Barnard, 1960, *H. percellaris* Barnard, 1971, *H. triplex* Barnard, 1971, and *Pseudharpinia excavata* (Chevreux, 1887) (Harpiniinae); and *Coxophoxus hidalgo* J.L. Barnard, 1966 (Coxophoxinae). Members of the bathypelagic subfamily Joubinellinae (e.g. *Joubinella strelkovi* Gurjanova, 1952) are expected to occur in deep offshore waters but have not been recorded from the region and are not treated here.

The history of the development of systematic knowledge of these free-burrowing phoxocephalid amphipods in North Pacific regional waters has been summarized by Jarrett & Bousfield (1994) and by Bousfield & Staude (1994). Briefly, very few records from the Asiatic coast existed prior to the work of Gurjanova (1938, 1951, 1953, 1977, 1980), or from the North American coast prior to the studies of J. L. Barnard (1957, 1958, 1960, 1971, 1979) and in co-authorship with Charlene Barnard (1980, 1981, 1982). Since then, work on the Asiatic coast has been expanded mainly by Hirayama (1987, 1992) and on the North American coast by Coyle (1982), and the present authors (Jarrett *et al.* 1990; Jarrett and Bousfield, 1994). The most significant single study affecting the higher level classification of North Pacific phoxocephalids was the monumental compendium on Australian Phoxocephalidae by J. L. Barnard and Margaret Drummond (1978), a work that has been basic to the present undertaking.

Despite the extensive contributions of previous workers on North Pacific phoxocephalid amphipods, a large gap has existed between the inshore material coverage of Barnard and co-workers in California and Oregon, on the one hand, and that of Gurjanova and colleagues in the far-eastern seas of the former Soviet Union, on the other. It is fortunate, therefore, that this geographical hiatus has to a large degree been filled by much new material from the region of coastal British Columbia and Southeastern Alaska, obtained mainly since 1955, through expeditions of the Canadian Museum of Nature in Ottawa (formerly the National Museum of Natural Sciences). The material, supplemented by other collections, particularly from the Bering Sea region, forms the basis of this report. About 300 lots of specimens from more than 150 sampling stations were examined, as ecologically detailed and mapped in the station lists of Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962), and Bousfield and Jarrett (1981).

The present study formally treats all the species occurring in this extensive material, classifies them in relation to previous work and to new taxonomic and phyletic concepts, and contributes to the solution of a number of problems in phoxocephalid systematics and distributional ecology that have been revealed during the course of the work.

ACKNOWLEDGEMENTS

This study could not have been completed without the help of many biological research agencies and interested colleagues. The field surveys were carried out with the full

support of the National Museum of Natural Sciences (now Canadian Museum of Nature) in Ottawa, and received vital technical assistance and ship-time from Canadian Pacific research centres and their staffs. These included the Pacific Biological Station, the Bamfield Marine Station, the Pacific Environmental Institute, the Royal British Columbia Museum, the University of Victoria, University of British Columbia, and the Institute of Ocean Sciences, Sidney, and, in the United States of America, the Friday Harbor Marine Laboratories and the College of Fisheries, University of Washington. Full acknowledgement to individuals of those agencies, and to many others, are provided in the previously published station lists (above), to whom we again express our deepest appreciation. For advisory assistance in preparation of this report, we are especially grateful to museum colleagues Kathleen E. Conlan and Ed Hendrycks, and for curatorial assistance especially to Ed, and to Judith C. Price. Preparation of the line illustrations was most capably assisted by Susan Laurie-Bourque, Hull, Quebec. Marjorie Bousfield provided translations of pertinent Russian literature. Work by the senior author, and by the artist, was also supported by operating grants from the Royal Ontario Museum, Toronto, and the Natural Sciences and Engineering Research Council, Ottawa.

SYSTEMATIC SECTION

The subfamily classification utilized here follows the system proposed initially for Australian phoxocephalids by Barnard and Drummond (1978) but modified by later studies on the world-wide fauna (e.g., Barnard and Barnard, 1982a; Barnard & Karaman, 1991). The arrangement of subfamilies is basically phyletic, as in Barnard & Drummond (1978), modified by phyletic principles developed on a broader basis across the Amphipoda in general (e.g. Bousfield, 1979, 1982, 1983; Schram, 1986; Bousfield & Staude, 1994; Jarrett & Bousfield, 1994). The technical format follows that of Barnard and Karaman (1991).

Although previous work on the systematics and classification of phoxocephalid amphipods has been extensive, relatively little significance has hitherto been placed on structures bearing on the reproductive process. The usefulness of character states of presumed mate-sensing structures of pelagic males, especially the antennal callynophore (Lowry, 1986) and calceoli (Lincoln and Hurley, 1981) has only recently been recognized, but not yet universally applied. Within the Phoxocephalidae some taxonomic attention has been paid to modifications in the form and armature of distal segments of pereopod 7 in the pelagic male (e.g. Barnard & Drummond, 1978) but their character states have seldom been incorporated into the classification of the species, or even utilized in keys to the species (e.g. Barnard & Barnard, 1981; Karaman, 1993). This copulatory apparatus, de-

FIG. 1. Phoxocephalid Subfamilies: Copulatory Spines of Male Pereopod 7.

(SEE PAGE 73 - OPPOSITE)

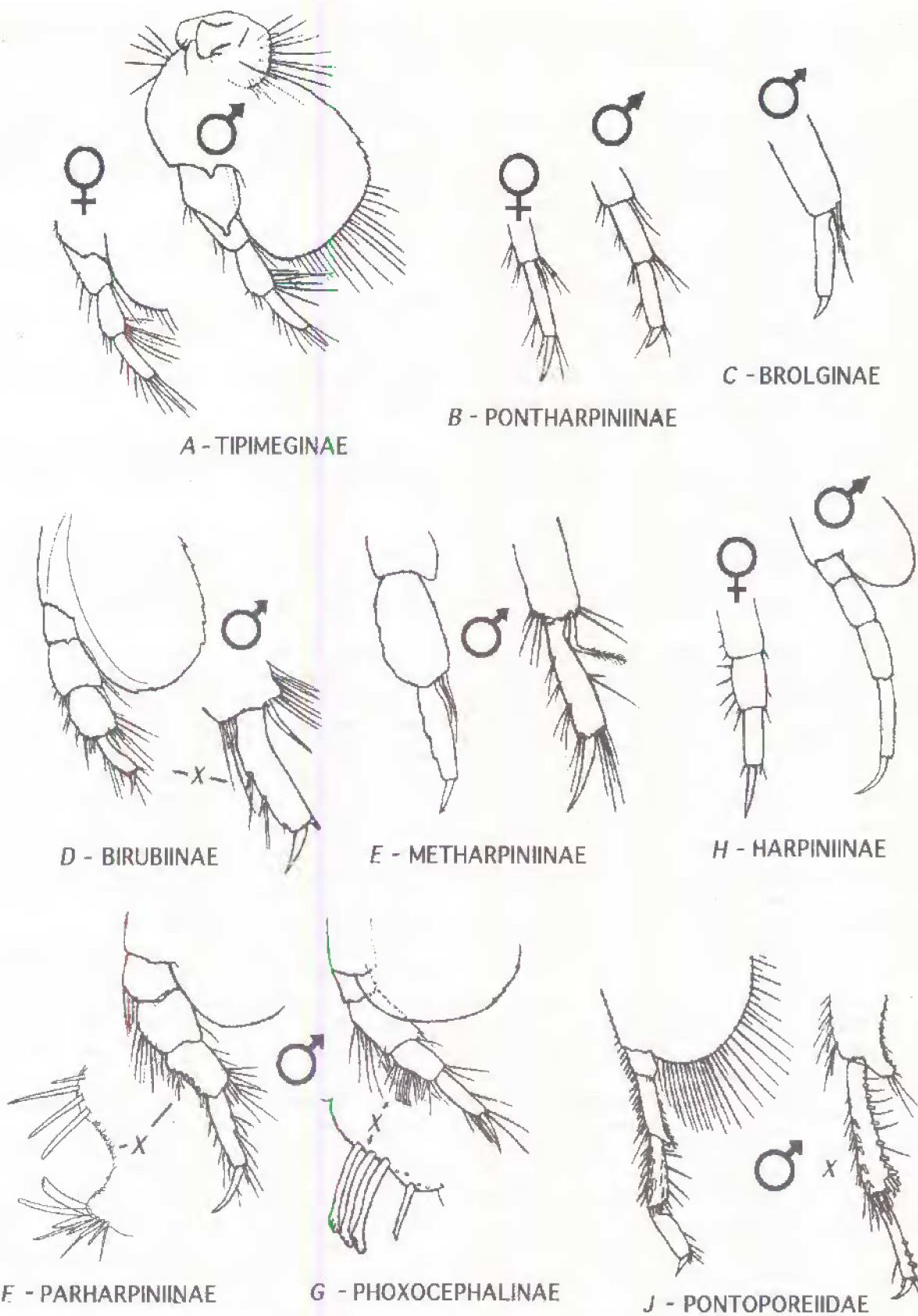


FIG. 1. PHOXOCEPHALID SUBFAMILIES: COPULATORY SPINES OF MALE PERAEOPOD 7

scribed below, is remarkably diverse across a spectrum of major subfamilies of the Phoxocephalidae (see Fig. 1, after Bousfield, 1990).

A presumed copulatory apparatus, consisting of specialized spines and/or modifications of some or all of the distal 4-5 segments of pereopod 7, occurs in final instar males. In these, the antennae usually bear calceolae and/or "brush setae" and the flagellum of antenna 2 may be elongate. In the more primitive subfamilies, e.g. Tipimeginae, Pontharpiniinae, Birubiinae, Metharpiniinae and Brolginae (Figs. 1A-E), one or two (rarely more) spines of the postero-distal spine cluster of segment 5 may be variously lengthened, thickened, sharply bent (deflexed), and/or distally pectinate, relative to the simple condition of comparable spines in the mature female. In the Birubiinae, one spine (or none) is conspicuously modified whereas in the closely related Metharpiniinae, two such spines, often of differing sizes, are more frequent.

Frequently associated with the presence of modified spines on segment 5, is a corresponding postero-proximal excavation or invagination of segment 6, near its junction with segment 5 (as in Brolginae, Birubiinae, and Metharpiniinae, figs. 1C-E). This segment, and the dactyl, are often shorter than those of the corresponding mature female, as in Tipimeginae, Pontharpiniinae, and Brolginae (Figs. 1A-C).

Within subfamilies Parharpiniinae and Phoxocephalinae, however (Figs. 1F, G), the anterior marginal spines of segment 5 are modified, often spectacularly so (see also Figs. 9-11 of *Eyakia* species). In these forms, the anterior margin of segment 5 is variously excavated or incised, thickened or corrugated, with one or more spines enlarged and robust, occasionally strongly curved or hook-like. The apices of these spines are often broadened and/or striated. However, segment 6 and the dactyl remain similar to those of the female. In the most advanced family, Harpiniinae, the distal segments of pereopod 7 of the male are relatively slender, lack specialized spines of any kind, but the dactyl is more slender, elongate, and strongly curved than in the female (Fig. 1H).

The function of this apparatus has apparently seldom been carefully observed in any species to date. However, its occurrence only in the reproductively active mature male instar (not in females or subadult males), its physical form, and its location on the hindmost pair of pereopods, strongly suggest that the mechanism functions during the copulatory embrace of the mating pair. A grossly similar apparatus, also on pereopod 7, of the phylogenetically unrelated, but morphologically and reproductively similar members of family Pontoporeiidae, has long been known (Fig. 1J, but see also Gurjanova, 1951, figs 205, 209). Such an occurrence might indicate that this phenomenon has evolved, convergently, at least twice within fossorial amphipods. In absence of critical observation, one is tempted to speculate on the mechanical functioning of this apparatus. Conceivably, it may help secure the female during actual copulation, and thereby perform, analogously, the principal role of the male gnathopods

in reproductively more advanced, pre-amplexing, amphipod groups. Alternatively, one might envision the spines assisting in holding apart the broad fossorial legs and side plates of the female in order to facilitate actual sperm transfer during copulation. However, these postulations merely underscore the critical need for careful studies on functional morphology and breeding biology of these remarkable animals.

PONTHARPINIINAE Barnard & Drummond

Pontharpiniinae Barnard & Drummond, 1978: 40.

Brolginae Barnard & Drummond, 1978: 87 (partim: *Mandibulophoxus*).

Harpiniinae Barnard & Drummond, 1978: 530 (partim: *Basuto*).

Type Genus. *Pontharpinia* Stebbing, 1897: 32.—Barnard & Drummond, 1978: 40. (= *Urophoxus* Gurjanova, 1977: 85).

Genera: *Basuto* Barnard & Drummond, 1978 [530]; *Mandibulophoxus* J. L. Barnard, 1957 [432]; *Griffithsius*, new genus [p. 76]; *Urophoxus* Gurjanova, 1977 [85].

Diagnosis: The principal distinguishing features of subfamily Pontharpiniinae include the following:

Head very short and deep; eyes small or lacking (both sexes). Rostrum very elongate, not incised laterally, inferior antennal sinus shallow. Antenna 1, peduncle 1 elongate, 2 shortened, 3 very short; flagellum and accessory flagellum multi-segmented; basal segments callynophorate in male; distal segments with elongate aesthetascs (calceoli on flagellum of A1, *vide* Barnard & Drummond (1978). Antenna 2 (male) short, flagellum short; segment 5 (male), inner face bearing 4 large barrel-(paddle)-shaped calceoli; segment 1, ensiform process weak or lacking.

Mandibular palp attached to large palpar hump (molar hump of Barnard & Drummond 1978); left lacinia 5-dentate, right lacinia flabellate, spine row often long. Maxilla 1, palp 2-segmented (or 1-segmented?); inner plate setose. Maxilla 2, plates small, facial setae lacking. Maxilliped, plates small, palp strong, dactyl long.

Gnathopods strongly subchelate; gnathopod 2, propod stronger, carpus shorter, than in gnathopod 1.

Pereopods 3 & 4 powerful; segment 6 may be spatulate. Pereopod 5, basis variously pyriform, distally broadened. Pereopod 6, segment 4 bulbous, proximally broadest. Pereopod 7, basis long and broad; segment 3 lengthened.

Pleopods not strongly sexually dimorphic; peduncles normal. Uropod rami linear, apically spinose; uropod 1 with distolateral spine. Uropod 3, rami elongate, plumose-setose, sexually subsimilar.

Telson lobes subapically spinose; penicillate setae proximal to medially inserted. Coxal gills sac-like, small on pereopod 7. Brood plate 5 slender, often broadened distally.

Taxonomic Commentary: The Pontharpiniinae comprises a very distinctive and specialized subfamily group that entrains both plesiomorphic and apomorphic character states. The austral subgroup of 3 genera appears more plesiomorphic than North American members in the presence of pigmented eyes, less strongly developed molar (palpar) hump, and aequiramous, plumose-setose uropod 3. A more comprehensive revision of this subfamily complex awaits the collection and analysis of further material, especially from the southern hemisphere, and especially the careful characterization of mature males of the austral genera.

The north Pacific genus *Mandibulophoxus* is apomorphic in these and most other character states. The pyriform shape of the basis of peraeopod 5 (in *Basuto*) may be narrowed superficially almost to the linear condition, a single character state which may have led Barnard & Drummond (1978) to mis-classify it within the Harpiniinae (see fig. 2). The genus *Mandibulophoxus* had been classified with the genus *Paraphoxus* Sars in subfamily Broilginae by Barnard and Drummond (1978) and maintained there by Barnard and Karaman (1991). Perceptively, they had noted its overall generic similarity to *Pontharpinia* (loc. cit., p. 90) but "overruled" such an alliance by the taxonomic weight they gave to an apparently dissimilar condition of the mandibular molar. Paradoxically, this range of molar character states was not deemed inimical to their phylogenetically correct decision to include (within subfamily Phoxocephalinae) such molar-disparate types as *Phoxocephalus* and *Limnoporeia*. Mindful of this precedent, the inclusion of *Mandibulophoxus* within the Partharpiniinae seems fully justified here.

Sexual dimorphism is relatively weakly expressed within the Pontharpiniinae. Thus, in antenna 2 of the male of *Mandibulophoxus*, the flagellum is short and non-calceolate, as in the female. However, peduncular segment 5 is broadened and bears 4 large, barrel-shaped calceoli on its inner surface. The condition of the male antennae in the other genera has not been critically described (e.g., in Barnard and Drummond, 1978; Griffiths, 1973; 1976a,b). However, the close similarity of antenna 2 of the female of *Pontharpinia*, *Basuto*, and *M. "latipes"* to that of *Mandibulophoxus* suggests that the condition of antennae 2 of the males of these genera is also similar. "*Mandibulophoxus*" *latipes* Griffiths (1976b) is so distinctive in the form of its peraeopods 3 & 4, and uropods 1 & 2, that a new genus is warranted for its reception, aligned naturally also within the Pontharpiniinae (see below).

Urophoxus Gurjanova (= *Pontharpinia* Stebbing)

Pontharpinia Stebbing 1897: 32 (*Urothoe pinguis* Haswell, 1879, monotypy).—Stebbing, 1906: 146 (part).—Barnard & Drummond, 1978: 40.

Type species: *Urothoe pinguis* Haswell, 1879, by monotypy.

Diagnosis: (Condensed from Barnard & Karaman, 1991). Eyes weakly pigmented. Rostrum distally downcurved. Mandible with 5-dentate left lacinia; palpar hump weak; molar triturative, small, margin spinose.

Gnathopod 1, carpus slender, elongate. Gnathopod 2, carpus short, hind lobe cryptic. Peraeopods 3 & 4 similar distally, segment 6 long, dactyl short. Peraeopod 5, basis medium, broad distally, segment 4 broader than deep.

Pleon plate 3, hind corner strongly hooked, falciform. Uropod 3, rami aequiramous, margins spinose-setose in female. Telson lobes with proximo-lateral setal clusters.

Taxonomic Commentary: The type species has been quite fully described and illustrated by Barnard and Drummond (1978, pp. 41-46, figs. 8-10). In mature males in their possession, they did find large calceoli on proximal flagellar segments of antenna 1. However, they did not describe calceoli on antenna 2, either on the peduncle or on the relatively short flagellar segments. Is it possible that the relative shortness of the flagellum in these males may have led to their belief that they were not "advanced" (ie. reproductively fully mature)? As in males of *Mandibulophoxus*, calceoli might very well have been present on antenna 2 but, not being marginal in position, may have been "concealed" against the face of segment 5 in unstained material. In this regard, therefore, it is suggested that this material be made available for re-examination.

Basuto Barnard & Drummond

Basuto Barnard & Drummond, 1978: 530.—Barnard & Karaman, 1991: 598.

Species. *Basuto stimpsoni* (Stebbing, 1908) (Barnard 1957 [436] fig. 4.)(Reid, 1951 [222])(Griffiths, 1974a,b). *Basuto* species (Griffiths, 1976b, figs. 39 D,G).

Diagnosis: (see Barnard and Drummond, 1978, loc. cit.). Eyes present, weakly pigmented. Mandible with medium strong palpar hump; molar reduced, with a few spines.

Gnathopods dissimilar in size, and otherwise typical of the subfamily. Peraeopods 3 & 4 subsimilar in size and form. Peraeopod 5, basis sublinear, weakly or narrowly pyriform, segments 4 & 5 not strongly broadened.

Pleon plate 3 rounded behind, ordinary. Uropod 2, rami slender, unequal, posterior margins spinose or smooth. Uropod 3 inaequiramous, inner ramus non-setose.

Telson lobes lacking lateral setal clusters, apices each with simple spine.

KEY TO GENERA OF PONTHARPINIINAE

1. Pigmented eyes present; mandibular palpar hump moderate; telson often with lateral setae; uropod 3, margins plumose-setose; Austral-S. African 2.
—Pigmented eyes lacking; palpar hump strongly developed (half the length of palp segment 2); telson laterally smooth; uropod 3, ramal margins spinose, or weakly setose; Asian-North American.
..... *Mandibulophoxus* (p. 77)
2. Pleon plate 3, hind corner produced, hook-like; telson with baso-lateral setal clusters; mandibular molar triturative *Urophoxus* (= *Pontharpinia*) (p. 75)
—Pleon plate 3 squarish or rounded behind; telson with single lateral seta; mandibular molar process reduced, 2-3 spine-tipped; African-Madagascar 3.
3. Peraeopods 3 & 4., segment 5 not shortened, segment 6 unlike in both; peraeopod 5, basis broadly pyriform; uropods 1 & 2, rami short and stout, with heavy distal spines. *Griffithsius* n. g. (p. 76)
—Peraeopods 3 & 4, segment 5 shortened (much shorter than segment 4), segment 6 alike in each; uropods 1 & 2, rami as long as peduncles, spined heavily throughout *Basuto* (p. 75)

Taxonomic Commentary: The species *Basuto latipes* (Griffiths, 1976) (Barnard & Karaman, 1991) is transferred to a new genus, *Griffithsius* (see below). The species illustrated by Griffiths (1976b) as *Mandibulophoxus stimpsoni* differs from *M. stimpsoni* as illustrated by Barnard (1957) and represents an unnamed species of *Basuto*.

Griffithsius, new genus
(Fig. 2)

Mandibulophoxus Griffiths, 1976: 27 (partim).

Type species. *Mandibulophoxus latipes* Griffiths, 1976b: 27, figs. 9-10 (here designated).—Barnard & Karaman, 1991 [598].

Species. *Griffithsius* sp. (= *Metaphoxus* sp. Griffiths, 1973 [296]).

Diagnosis: Generally similar to *Basuto* but with the following combination of character states:

Rostrum narrowly hood-like, very elongate, down-turned apically. Eyes small, weakly pigmented. Antenna 1, flagellum elongate, with weak basal calynophore (male). Antenna 2, peduncular segment 4 expanded and setose posteriorly; flagellum not elongate in male(?).

Mandibular palpar hump short; molar lacking, spine row long; palp expanding distally, with strong apical spine cluster. Maxilla 1, palp 2-segmented (or indistinctly so?), distal segment oblique, slender-spinose or setose; inner plate with 3-4 apical setae. Maxilliped plates short; palp, segment 4 (dactyl) elongate.

Gnathopods stoutly subchelate. Gnathopod 1 propod the smaller; palm of propod short, nearly vertical; carpus elongate. Gnathopod 2, carpus short, hind margin cryptic, palm of propod oblique, smooth.

Peraeopods 3 & 4 differing markedly; in peraeopod 3, segments 4, 6 and 7 (dactyl) relatively short, segment 6

spatulate, strongly spinose behind or reduced; in peraeopod 4, segments 4, 6, and 7 normal or elongate, segment 5 relatively short. Peraeopod 5, basis pyriform, broadening distally, segments 4 & 5 broad. Peraeopod 6, segment 4 little expanded posteriorly.

Pleon plate 3 quadrate behind, not hooked or falciform; outer face variously setose. Uropods 1 & 2, rami short, stout; rami strongly spinose posteriorly and apically; uropod 1 with displaced spine. Uropod 2, rami markedly unequal (outer shorter). Uropod 3 aequiramous, variously plumose-setose (both sexes).

Telson lobes each with apical spines only.

Etymology: Named in honour of Charles Griffiths who has significantly advanced knowledge of marine and freshwater amphipods of the greater South African region.

Taxonomic and Distributional Commentary. The type species (*latipes*, above) figured by Griffiths (1976) is unquestionably pontharpiniid in every feature, including the pyriform shape of peraeopod 5 basis, and the typically deeply lobate basis of peraeopod 7. However, Griffiths (1973) placed a single undetermined, larger male specimen (Stn. PED 18 V) questionably in the genus *Metaphoxus*, based on what he believed to be a 1-segmented palp of maxilla 1. However, his observations on maxilla 1 require confirmation, as the palp may be indistinctly 2-segmented in pontharpiniid species. In all other features, the animal is clearly pontharpiniid, including the very long downcurved rostrum, elongate primary and accessory flagellum, with short, obtusely angled, peduncular segment 3, short peduncular segments 3 & 4 of antenna 2, subequal rami of uropod 3 (outer segment short), and form of the mandible. The gnathopods are typically pontharpiniid. In Fig. 10 (*Ibid.*, 1973), peraeopod 7 is apparently not shown. Instead, what appear to be the distal segments (4, 5, 6, and 7) of peraeopod 5 are illustrated. Segment 4 (mistakenly described as segment 2 of peraeopod 7) is much expanded; segments 5, 6, & dactyl are short and slender.

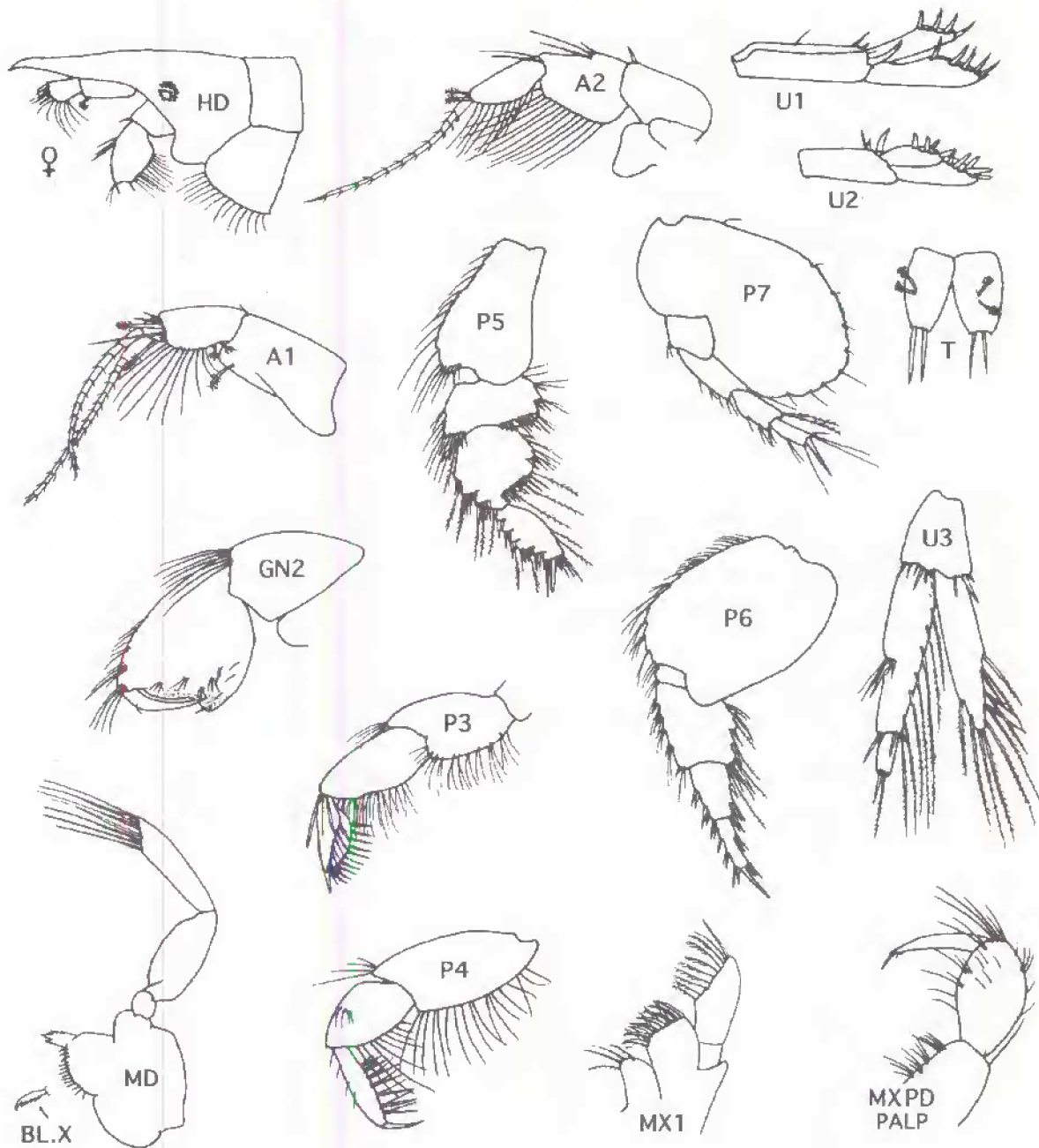


FIG. 2. *Griffithsius latipes* (Griffiths) ♀ (7.0 mm) S. W. Africa.
(modified from Griffiths, 1976).

Mandibulophoxus J. L. Barnard

McCain, 1969 [189].

Mandibulophoxus Barnard, 1957: 432.—Gray & McCain, 1969: 189.—Barnard & Drummond, 1978: 90.—Barnard & Karaman, 1991: 619.

Type species: *Mandibulophoxus gilesi* Barnard, 1957, original designation.

Species: *Mandibulophoxus alaskensis*, new species [p. 80]; *M. mayi*, new species [p. 81]; *M. uncistrostratus* (Giles, 1890 [65]); (J.L. Barnard, 1957 [435]); (Gray &

Diagnosis: With the characters of the subfamily. Rostrum elongate, unstricted. Pigmented eyes lacking or vestigial. Antenna 1, flagellum and accessory flagellum multisegmented; peduncular segment 2 short, posterior marginal setae confined distally; segment 3 very short, unarmed. Antenna 2, segment 1 normal (not ensiform); segment 3 with 2 setules; segment 4 deeper than 5, both spinose behind. Antennae of male shorter, with fewer flagellar segments; antennae 2, peduncular segment 5 deep, with 4 very large medial facial calceoli inserted near posterior margin.

KEY TO NORTH AMERICAN PACIFIC SPECIES OF *MANDIBULOPHOXUS*

1. Peraeopod 7, basis broader than deep, lower margin with 10-14 setae; uropods 1 & 2, rami as long as (or longer than) peduncles, each with 4-5 regularly acute spines; telson lobes apically with 3 spines; male calceoli broadest medially 2.
- Peraeopod 7, basis less elongate, about as deep as broad, lower margin with 6-8 setae; uropods 1 & 2, rami unequal, shorter than peduncles, each with 2-3 short, stout, blunt spines; telson lobes apically with 2 spines; male calceoli tapered, broadest distally *M. alaskensis*, n. sp. (p. 80)
2. Gnathopods stout, carpus of gnathopod 1 not longer than propod; peraeopod 5, basis lined posteriorly with 20-30 short setae; uropod 3, inner marginal setae simple *M. mayi*, n. sp. (p. 81)
- Gnathopods slender, carpus of gnathopod 1 longer than propod; peraeopod 5 basis lined posteriorly with 35-50 short setae; uropod 3, inner marginal setae of rami plumose . . . *M. gilesi* Barnard (p. 78)

Upper lip, epistome not produced. Lower lip broad, squat, outer lobes with cones. Mandible, molar of B & D type, with 3 apical spines; blades 6-8, ordinary, alternating with smaller blades; left lacinia 6-8 dentate, flabellate; right lacinia lacking; left incisor 10-cusped; right incisor 5-6 cusped; mandibular body with large palpal hump; palp segment 3 lacking "A" and "C" setae (of Cole, 1980). Maxilla 1, outer plate with apical spines, inner plate 3-5 setose; palp broad. Maxilla 2, inner plate small, with distal sub-marginal (facial?) row of slender pectinate spines. Maxilliped, plates narrow, small, inner lacking apical conical spines; palp large, inner margin often spinose; dactyl slender, longer than segment 3.

Coxae 1-3, lower margins moderately to strongly setose; coxae 4 very broad. Gnathopods 1 & 2 unequal, regularly subchelate, 2 little larger. Gnathopod 1, carpus elongate, subequal to propod. Gnathopod 2, carpus short, length about half propod.

Peraeopods 3 & 4, similar in size and form; segment 4 expanding distally, 5 short, stout, segment 6 spatulate; dactyl slender. Peraeopod 5, basis broadening distally, pyriform; segments 4 & 5 broad, 6 slender. Peraeopod 6, basis broadly rounded; segment 4 proximally very broad, segments 5-7 tapering distally. Peraeopod 7, basis hind lobe very broad and deep, exceeded below only by segment 6 and dactyl; dactyl may be short in male.

Pleon plate 2 smooth behind, setose anteriorly below; pleon 3 squarish and weakly cusped and setose behind. Uropods 1 & 2, inner ramus the shorter; rami with few stout distal marginal and apical spines; peduncle of uropod 1 with stout disto-lateral spine. Uropod 3 slender, inner ramus medium long; inner margin of rami usually setose (both sexes).

Telson lobes medium broad, apices rounded, each with 2-3 strong spines but no lateral stae. Brood plates slender, with long distal setae. Coxal gills slender, simple, smallest on peraeopod 7.

Taxonomic Commentary: Difference between the N. American *M. gilesi* and the Indian subcontinental *M. uncistrostratus* were noted and confirmed at species level by

Barnard (1957) and Gray & McCain (1969). They examined only one N. American species and, in limited material, detected no males.

The unusual form of calceolate armature of antenna 2 in males of *Mandibulophoxus* is yet unknown elsewhere within the Phoxocephalidae. Such a remarkable condition may be unique within the genus, or possibly endemic to the Pontoharpiniinae. Regretably, however, the calceoli of males of other genera of this subfamily have not yet been described.

Distribution: Members of this genus are widely distributed along N. American Pacific shores, in fine organic sands, from S.E. Alaska to southern California (see Table I).

Mandibulophoxus gilesi, J. L. Barnard
(Figs. 3,4)

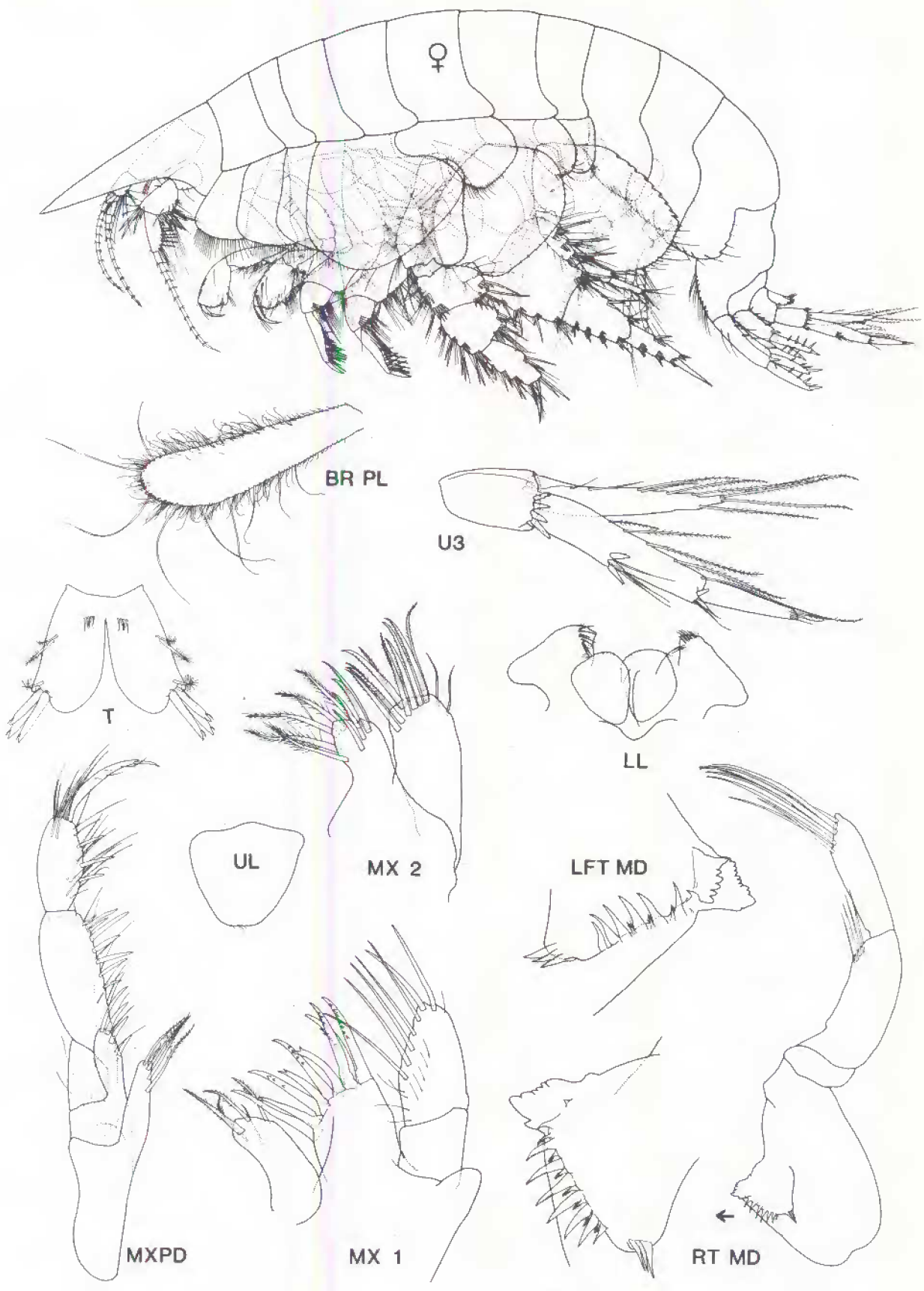
Mandibulophoxus gilesi Barnard, 1957: 433 (figs.1-2).—Gray and McCain, 1969: 189 (fig. 1).—Barnard & Drummond, 1978: 91 (Key).

Mandibulophoxus uncistrostratus Barnard, 1960: 359 (partim).—Barnard, 1969: 196 (partim).

Material Examined: More than 400 specimens, about 5/8 females (mostly ovigerous) from 14 stations, at or slightly below LW level, along open sandy beaches, ranging north from central California and Oregon to the Strait of Juan de Fuca. CMN collections, as follows:

BRITISH COLUMBIA: Vancouver Island; Experiment Bight, Cape Scott, ELB Sta 01, July 18, 1959. - 1 female, 3 males; Grant Bay, Quatsino Sound, ELB Sta. O3, Cape Scott, July 21, 1959 - ~ 30 specimens; Clo-oose, outer coast, ELB Stn. P713, main beach, steep coarse sand, July 23, 1970. - 1 female, 4 males.

FIG. 3. *Mandibulophoxus gilesi* Barnard, 1957.
FEMALE ov. (6.0 mm)
(SEE PAGE 79 - OPPOSITE)



WASHINGTON: ELB Stns, 1966: W35 (Juan de Fuca region); W14, W20 (Gray's Harbor region); W18, W46 (Willapa Bay region) - 90 females, 115 males;

OREGON: ELB Stns, 1966: W53, W61, W63 (Tillamook region) - 67 females, 94 males (includes figured male and female specimens from Stn. W61, CMN. Cat. No. NMCC1992-1000.

Diagnosis: Female (6.0 mm): Antenna 1, flagellum and accessory flagellum 9-11-segmented. Antenna 2, peduncular segment 5 little expanded, hind margin with 6-8 stout spines; flagellum 10-11-segmented.

Mandibular molar, right incisor 7-dentate; left incisor 10-dentate; palp segment 2 broader than 3, with distal submarginal row of 4 setae. Maxilla 1, outer plate with 9 apical spines, inner plate with 5 apical setae. Maxilliped, palp segments 2 & 3, inner margin of each lined with several stout spines; outer plate extending beyond palp segment 1, inner margin with 4 stout spines.

Coxa 1 slightly deeper anteriorly, lower margin with 20+ setae. Coxa 4 distinctly broader than deep. Gnathopods slender; gnathopod 1, carpus longer than propod.

Peraeopod 5, hind lobe of coxa broad below, longer than deep; basis not excessively narrowed proximally, lined posteriorly with 35-50 short setae. Peraeopod 6, basis broadest medially, anterior margin not proximally incised. Peraeopod 7, basis elongate, posterior margin with 8-9 distinct notches, lower margin with 10-14 setae; segments 5 & 6 subequal.

Pleon plate 3, lower margin convex, lined with 6-8 slender spines. Uropods 1 & 2, rami nearly subequal, outer shorter than peduncle, each distally with 4-5 heavy acute spines. Uropod 3, inner ramus and proximal segment of outer ramus are subequal in length, inner margins of both rami are weakly plumose-setose.

Telson lobes each with 3 apical spines, 1 shorter. Coxal gills slender, smallest on peraeopod 7.

Brood plate of peraeopod 5 broadening distally.

Male (4.5 mm.): Differing mainly in the form and armature of the antennae, armature of uropods 1-3, and telson. Antenna 1, flagellum 9-segmented, segment 1 conjoint, elongate, forming weak callynophore, with postero-distal cluster of 5-6 long aesthetascs; accessory flagellum 8-segmented. Antenna 2, peduncular segments 4 and 5 each with 5 heavy postero-distal spines; calceoli paddle-shaped, basally broad; flagellum 9-segmented. Peraeopod 7, dactyl very short, <1/4 propod. Uropod 3 rami only slightly more setose marginally than in female.

Distributional-ecological commentary: The species occurs mainly along open surf coasts in fine sand, from LW level to shallow subtidal depths and subtidally in substrata exposed to tidal currents. *M. gilesi* ranges from central British Columbia to southern California. Males are present in July and August in the northern part of the species range.

Mandibulophoxus alaskensis, new species
(Figs. 5, 6)

Material Examined:

ALASKA: South-eastern Alaska, ELB Stn. A81, Hawkins Island, Orca Inlet, fine sand at LW, June 29/61: Lot #1 - female (5.0 mm), with slide mount (fig'd), HOLOTYPE, CMN Cat. No. NMCC1992-1104; male (4.5 mm), with slide mount (fig'd), ALLOTYPE, CMN Cat. No. NMCC1992-1105; 43 female (mostly ov.), 29 male PARATYPES, CMN Cat. No. NMCC1992-1106. Lot #2 (dried specimens) - 20 females (mostly ov.), 19 male PARATYPES (combined, above).

BRITISH COLUMBIA: Saanich Inlet, K E Conlan coll., Mar. 14, 1975 - 1 female ov. (5.0 mm) with slide mount (variation fig'd?), CMN. Cat. No. NMCC1992-1107. Haro Strait, NW James I., D.V. Ellis Sta. 2403, Mar. 8, 1979. - 1 male (4.5 mm), 1 subadult male (4.5 mm), CMN Cat. No. NMCC1992-1108.

Diagnosis: Female ov. (5.0 mm): Antenna 1, flagellum and accessory flagellum 8-9 segmented. Antenna 2, flagellum 8-11 segmented; peduncular segment 4 with 7, and segment 5 with 5, stout posterior marginal spines.

Mandibular palp, segment 2 with 2-3 inner distal setae; left lacinia 5-6 dentate; blades 6-8, distal blade of right mandible forming a short bifid pseudo-lacinia. Maxilla 1, outer plate with 11 apical spines; inner plate with 4 apical plumose setae. Maxilliped, palp segment 2 with 2-3 distal inner marginal spines; outer plate exceeding palp segment 1, inner distal margin with 3-5 stout raptorial spines.

Coxa 1 expanding distally, weakly hatchet-shaped, distal margin with 10-12 setae. Coxa 4 about as wide as deep, posterior excavation shallow, hind lobe very broadly rounded. Gnathopods relatively stoutly developed. Gnathopod 1, carpus not longer than propod.

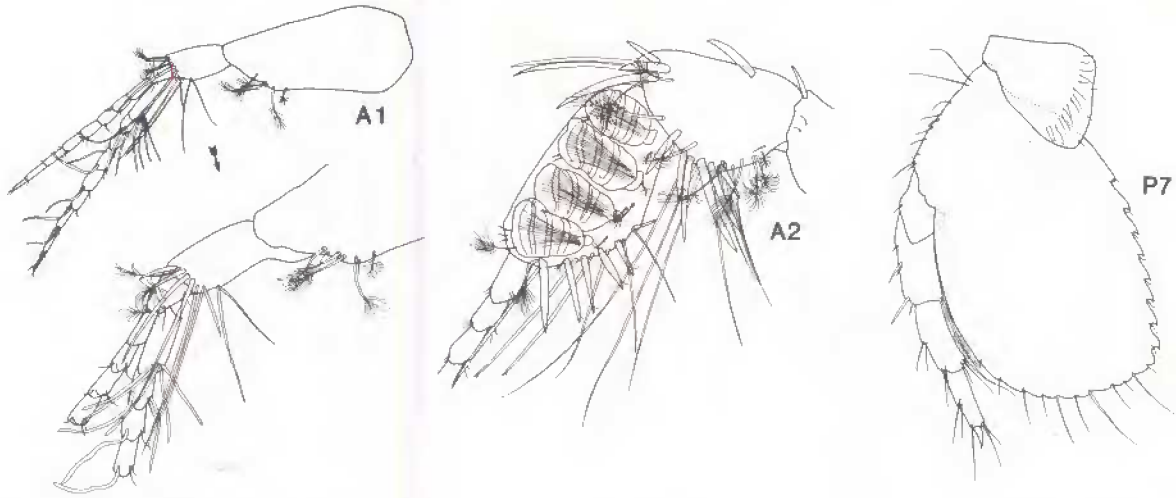
Peraeopod 5, hind lobe of coxa medium deep, broadly rounded below; basis narrow proximally, hind margin weakly setose (12-18 setae). Peraeopod 6, basis broadest medially, anterior margin unindented. Peraeopod 7, hind lobe deeper than broad, hind margin with 6-8 weak serrations, lower margin with 6-8 setae.

Pleon plate 3, lower margin convex, with submarginal row of 5-6 slender spines; hind margin with 4-6 setae, one large. Uropods 1 & 2, rami short, outer ramus shorter than peduncle but distinctly longer than inner ramus; rami distally with 2-3 short, stout, often blunt-tipped spines. Uropod 3, inner ramus distinctly shorter than proximal segment of outer, distal segment short (<1/3 proximal); inner margins of rami with a few plumose setae.

FIG. 4. *Mandibulophoxus gilesi* Barnard, 1957.

MALE (4.5 mm)

(SEE PAGE 81 - OPPOSITE)



Telson lobes each with two subequal apical spines.

Male (4.5 mm): Antenna 1, flagellum 7-segmented, basal segment weakly conjoint, length equal to two successive segments, postero-distally with cluster of 7-8 elongate aesthetascs. Accessory flagellum 7-segmented. Antenna 2, peduncular segment 4 with 5, and segment 5 with 4 strong posterior marginal spines; calceoli balloon-shaped (proximally narrow, distally broadest); flagellum 7-9-segmented. Pereopod 7, dactyl normal, about half length of propod.

Taxonomic and biogeographic commentary: *Mandibulophoxus alaskensis* is distinct from *M. gilesi* in characters noted in the key and text (above). The differences hold in both males and females. Moreover, the distributions are essentially disjunct, overlapping only in the Vancouver Island region. The northern species may yet be found in suitable localities to the west and northwest of Prince William Sound, and to the south in northwestern British Columbia. Recent surveys (Slattery & Conlan, personal communication) suggest that bottom faunas were not seriously affected, let alone extirpated, by the great Exxon oil spill of 1989, and full re-establishment of subtidal populations may soon be completed.

Subtidal specimens from Saanich Inlet and Haro Strait show slight variations in setation of pereopod bases, and armature of uropods, etc., but numbers are too few to assess the range of variation and hence the level of taxonomic significance. However, in a female (5.0 mm) from Saanich Inlet (fig. 6), the following differences (from Alaska females of similar size) were noted:

Gnathopod 1, superior lateral setae of propod in 4-5 groups; pereopod 5, basis, posterior marginal setae short, close-set, 10-12 in number; brood plate of pereopod 5, margins with short supernumerary setae; pereopod 7, basis slightly broader, with 5-6 posterior serrations and 5-6 postero-distal setae; uropods 1 & 2, marginal and apical spines less slender, more blunt; uropod 3, inner margin of inner ramus with fewer plumose setae; telson lobes each with one short and one long stout spine.

Mandibulophoxus mayi, new species
(Fig. 7)

Material Examined:

BRITISH COLUMBIA: North-central coast: ELB Stn.H11, 1964 (Calvert I.) - 2 females, 1 male. Vancouver Island, outer coast: ELB Stn. P703, 1970 - 1 female ov., with slide mount, (HOLOTYPE), CMN Cat. No. NMCC1922-1101; 1 mature male, with slide mount, (ALLOTYPE), CMN Cat. No. NMCC1992-1102; *ibid.* - 100 females (many ov.), 71 males, PARATYPES, CMN CAT. NO. NMCC1992-1103; ELB Stn. P10, 1975, and P. Slattery, 1983, 25-30 m. (off Long Beach) - 4 females ov. Other material from: ELB Stn. H44, 1964; P711, 1970; B19b (Brady's Beach), 1977 - 141 females (mostly ov.), 89 males. Also ELB Stns., 1975: P21 (Bordelais Ids.), 30 m. - 3 females (ov.); P14a (Kecha Bay), 4-12 m. - 3 females, 9 males. ELB Stn. H41 (Jordan R.), LW, 1964 - 1 female, 1 male.

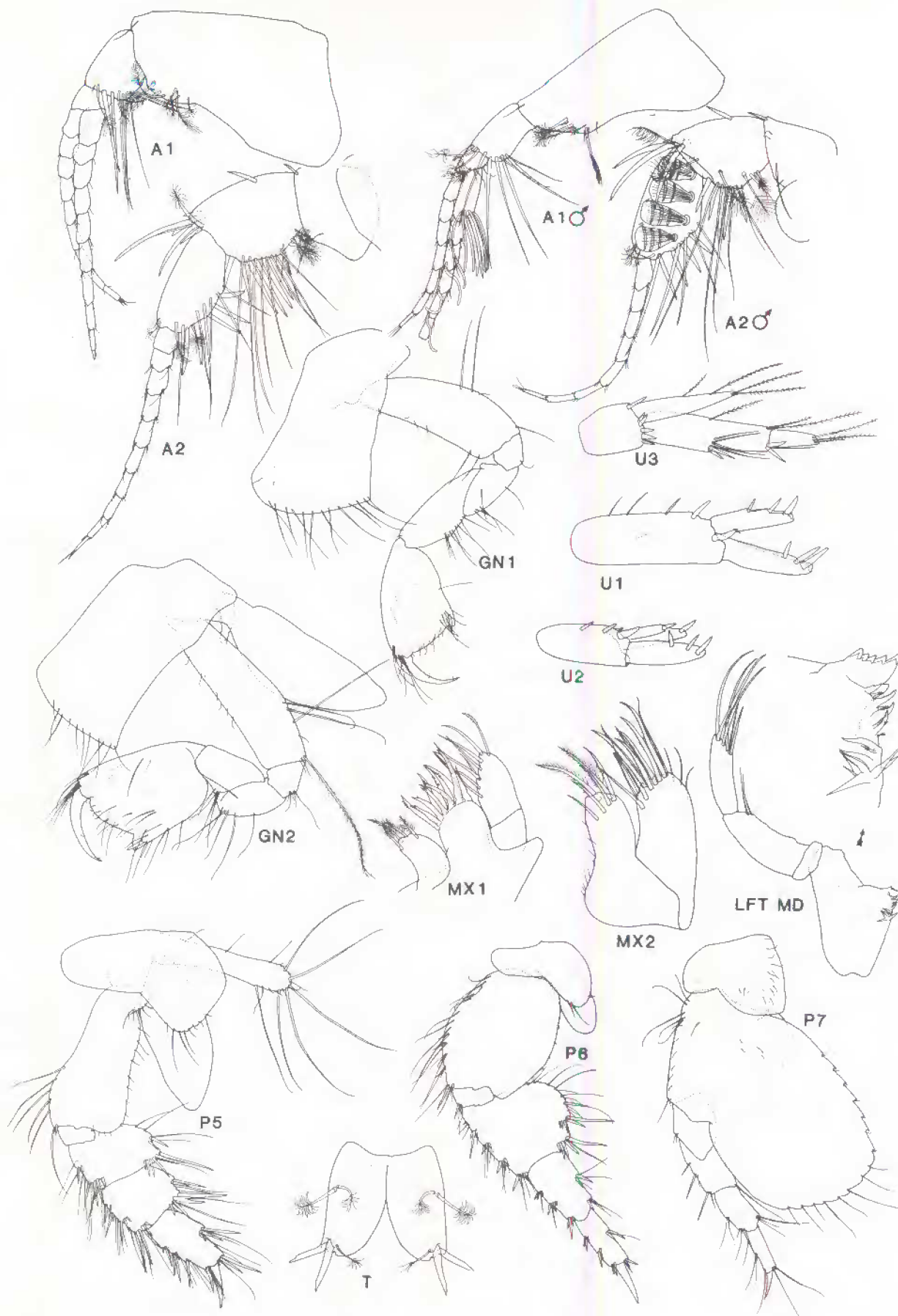
Diagnosis. Female (3.5 mm.): A small species with features mainly of the *M. gilesi* type. Antenna 1, flagellum and accessory flagellum 7-8 segmented. Antenna 2, flagellum 9-10 segmented.

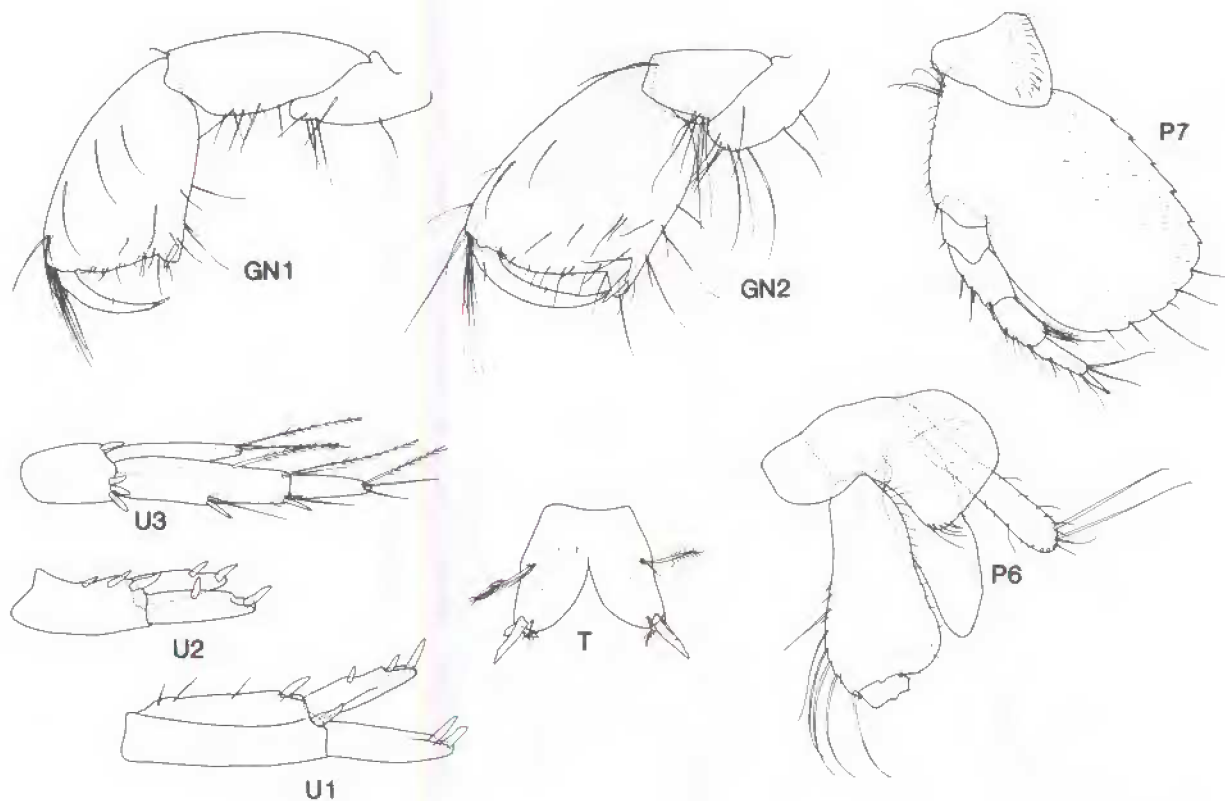
Mandibular palp, segment 2 with 2-3 inner distal setae; left lacinia 6-dentate; blades 5-7. Maxilla 1, outer plate with 9 apical spines, inner plate with 4 apical setae. Maxilliped, palp segment 2 distally with 2-3 inner marginal spines; outer plate short, not extending beyond palp segment 1, inner margin distally with 3 stout spines.

Coxa 1 slightly expanded antero-distally, not hatchet-shaped; coxa 4 little wider than deep. Gnathopods stout; carpus of gnathopod 1 distinctly shorter than basis and not longer than propod.

FIG. 5. *Mandibulophoxus alaskensis*, new species
FEMALE ov. (5.0 mm), HOLOTYPE;
MALE (4.5 mm), ALLOTYPE. (SEE PAGE 82)

FIG. 6. *M. alaskensis* var. FEMALE ov. (5.0 mm)
Saanich Inlet. B. C. (SEE PAGE 83)





Peraeopod 5, hind lobe of coxa deep, narrow; basis narrow proximally, length about $2\frac{1}{2}$ X distal width, hind margin with 25-30 close-set setae. Peraeopod 6, basis widest distally, anterior margin weakly incised proximally. Peraeopod 7, basis elongate posteriorly, hind margin with 5-6 weak serrations, junction with convex lower margin sharply angled, lower margin with 10-13 medium setae; segments 4-6 with slender anterior marginal spines.

Pleon plate 3, lower margin nearly straight, with 3-4 submarginal spines. Uropods 1 and 2, ramal pairs long, outer equal in length to peduncle, each distally with 4-5 regular, acutely tipped marginal spines and single stouter apical spine; peduncle with very stout distolateral spine. Uropod 3, inner ramus nearly equal to first segment of outer ramus, with single inner marginal and apical simple setae.

Telson lobes each with 3 subequal apical spines.

Brood plate on peraeopod 5 not expanded distally.

Male (3.5 mm). Antenna 1, flagellum 8-segmented, first conjoint, about equal in length to next three segments combined, bearing postero-distal cluster of 8 long aesthetascs; accessory flagellum 8-segmented. Antenna 2, flagellum 9-segmented; peduncular segment 4 with 7 stout postero-distal spines; segment 5 with 5 postero-distal spines and 4 median facial balloon-shaped calceoli.

Peraeopod 7, basis with 5-6 weak posterior marginal notches; dactyl about $\frac{1}{4}$ length of propod. Uropod 3, inner

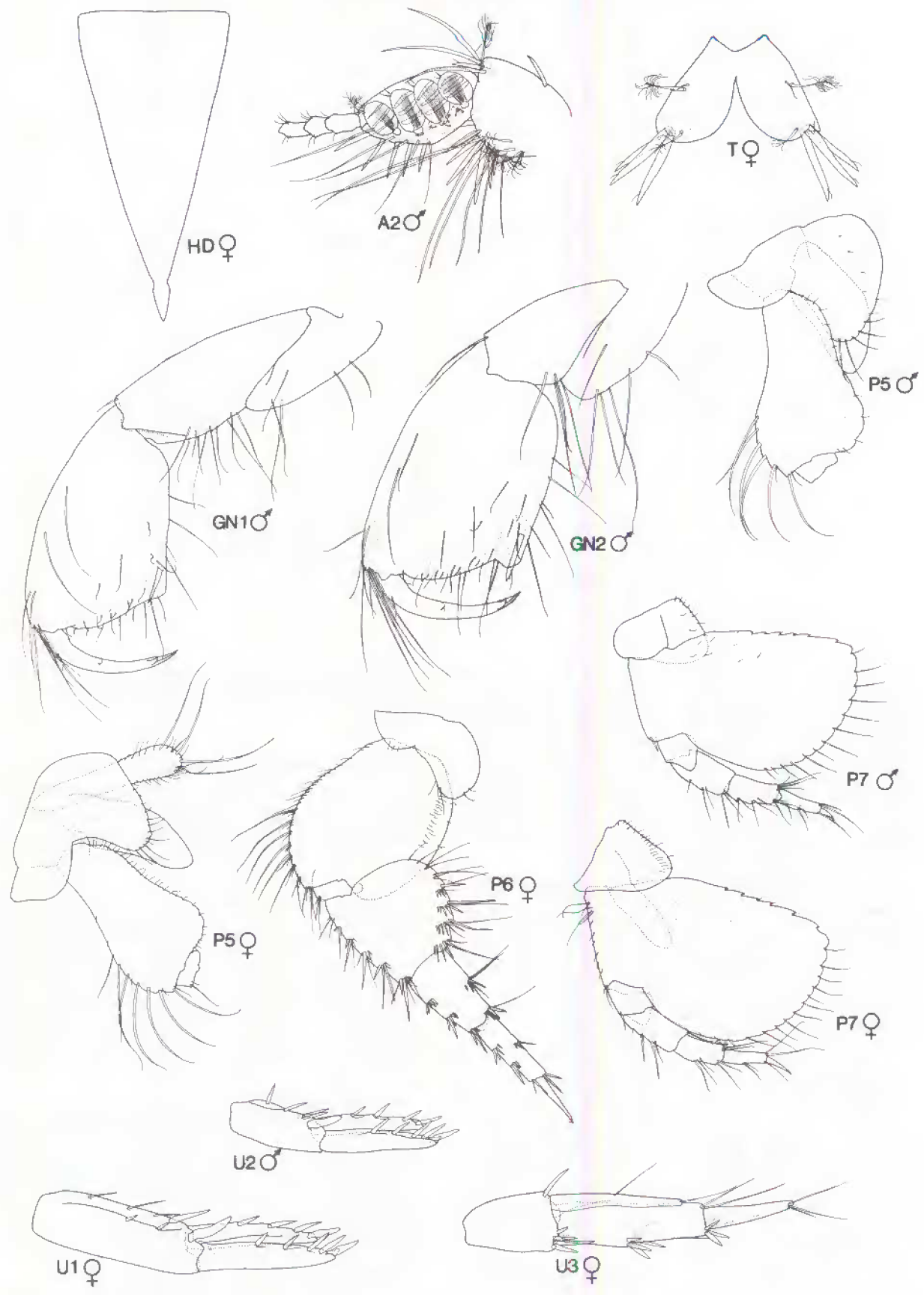
ramus longer than peduncle, with single simple inner marginal seta.

Etymology: Named in honour of Dr. Arthur S. May, former President and Chancellor, Memorial University, St. John's, Newfoundland, and former President, Natural Sciences and Engineering Research Council, for his outstanding support of aquatic biological research in Canada.

Taxonomic Commentary: *M. mayi* is most closely related to *M. gilesi* in the form and armature of the peraeopods and uropods, in the type of antennal calceoli (male), and in the form of the brood plates (female). Specimens from offshore, Long Beach, Vancouver Island, B. C. (Slattery material) differ slightly from the others in size and some minor features not here considered to be taxonomically significant.

Distributional Commentary: This species is common along open beaches of the southern and central coast of British Columbia, from the lower intertidal, subtidally to medium depths (30 m.). It overlaps distributionally with *M. gilesi* (but does not co-occur in the same habitats with it) throughout much of its known range.

FIG. 7. *Mandibulophoxus mayi*, new species
FEMALE ov. (3.5 mm) HOLOTYPE;
MALE (3.5 mm) ALLOTYPE. (SEE PAGE 84)



Parharpiniinae: Barnard & Drummond, 1978: 174 (part).—
Barnard & Karaman, 1991: 595 (key to genera).

Type genus: *Parharpinia* Stebbing, 1899: 207.

Other Genera: *Protophoxus*, K. H. Barnard, 1930: 335;
Eyakia, J. L. Barnard, 1979b: 375; *Phoxorgia* J. L. & C. M.
Barnard, 1980: 867.

Diagnosis: Rostrum fully hooded, elongate. Eyes small
or lacking in female, very large, pigmented, in male.

Antenna 1, peduncular segment 2 long; proximal seg-
ments of flagellum calceolate in male. Antenna 2, peduncular
segments 4 & 5 with facial and marginal clusters of stout
spines; segment 5 and elongate flagellum strongly calceolate
in male.

Mandible, molar process not triturative, apex with articu-
lated serrate spine(s); spine row strong; right lacinia bifid or
trifid, left lacinia irregularly 4-5 dentate; palp segments 2 &
3 slender, 3 usually with baso-facial setae. Maxilla 1, inner
plate with 1-4 apical setae; outer plate with 11 apical spines,
palp 2-segmented. Maxilla 2, plates subequal. Maxilliped,
palp powerfully raptorial, dactyl long; outer plate tall, inner
plate short, with 1-2 apical spines and setae.

Coxal plates 1-4 deep, not very broad, lower margins
usually strongly setose. Gnathopods regularly subchelate,
propods subequal, carpus with free lower margin.

Peraeopods 3 & 4 strong; segment 5 with strong postero-
distal spine; dactyls medium. Peraeopod 5, basis broad,
narrowing distally; segments 4-6 spinose not greatly ex-
panded, margins generally strongly setose and spinose.
Peraeopod 6 elongate; basis irregularly broad; segments 4-6
not broadened. Peraeopod 7, basis very broad, plate-like;
segments 4 & 5 somewhat broadened, margins setose; in
male, segment 5 of specialized copulatory form; anterior
margin variably incised, and lined with spines of specialized
form; one or two spines may be enlarged, curved, and striated
or otherwise modified at the apex.

Pleopods strong, rami long. Pleon plates 1-3 broad, lower
margins setose. Pleon 3, outer margin usually with facial
row of seta; hind corner often produced, tooth-like.

Uropods 1 & 2 powerful, rami tapering, marginal and
apical spines distinct, not shortened or fused with rami.
Uropod 1, peduncle with special apical spine Uropod 3
(female), rami unequal but outer ramus with setose margins;
in male, rami subequal and fully plumose-setose, terminal
segment short or lacking.

Telson lobes broad, apical spines few, short. Coxal gills
plate-like on peraeopods 2-6, smaller, sac-like on peraeon 7.

Taxonomic and Distributional Commentary: One
genus of this subfamily, *Eyakia*, is endemic to Asiatic and
North American shores of the North Pacific. A key to world
genera is provided by Barnard & Karaman, 1991, p. 595.

Eyakia J. L. Barnard, 1979b: 375.— Barnard & Barnard,
1981: 305.— Barnard & Karaman, 1991: 608.

Mesophoxus Gurjanova, 1977: 77.

Type species: *Parharpinia calcarata* Gurjanova, 1938b
(original designation).

Species (North Pacific region): *Eyakia robusta* (Holmes,
1908); *E. ochotica* (Gurjanova, 1953); *E. uncigera* (Gur-
janova, 1938b); *E. subuncigera* (Gurjanova, 1938b); *E. lap-
erusi* (Gurjanova, 1977); *Eyakia* species 1 (= *E. calcarata*,
Barnard, 1960); *Eyakia* species 2 (= *E. robusta*, large Aleu-
tian form, Barnard & Barnard, 1981).

Diagnosis: Rostrum entire, not or little incised in front of
eyes. Antenna 2 (male), segment 5 with 7 anterior marginal
calceoli; flagellar segments regularly calceolate; in female,
segment 4 with facial spines in 2 rows.

Mandibular palpal hump distinct; molar with 1-3 spines;
palp segment 3 usually with single baso-facial setal cluster.
Maxilla 1, inner plate with 4 apical setae. Maxilliped, inner
plate with 1 apical stout spine and 1 outer narrow spine.

Coxal plates, distal margins often heavily setose.
Gnathopods regular, carpus of gnathopod 1 the longer.

Peraeopods 3-4 strongly setose and spinose posteriorly.
Peraeopod 5 small, segments 4 & 5 not much broadened,
segments 5 & 6 subequal in length. Peraeopod 6, basis
shallowly concave behind; distal segments little broadened.
Peraeopod 7, hind margin of basis with numerous small
teeth. Segment 5 (male) usually with strong anterior marg-
inal copulatory notch and clasping spine.

Pleon plate 3, hind corner usually produced acute, outer
face with single row of long setae. Uropod 1, peduncle with
strong baso-facial setal row, but lacking displaced spine.
Uropod 2, peduncle with strong outer marginal spine row.
Uropod 3, rami short, nearly bare in female; in male, outer
ramus slightly the shorter, all margins plumose-setose.

Telson lobes medium long, apices with 1-3 spines, un-
equal in the female, subequal in the male.

Coxal gills large, plate-like, smallest on peraeopod 7.

Distributional Commentary: Members of the genus are
confined to the coastal waters of the North Pacific shelf
region, from immediately subtidal to depths of nearly 700 m.
At least three species occur along the N. American Pacific
shelf, from the Aleutians to Baja California.

Taxonomic commentary. The genus appears to be well
represented along both Asiatic and North American Pacific
shores. Numerical taxonomic analysis of component spe-
cies was not attempted because study material was available
for only one species. However, the group appears divisible
into two major subgroups. The *robustus* subgroup, occur-
ring on both sides of the Pacific, is marked by a strongly

KEY TO KNOWN SPECIES OF *EYAKIA*

1. Pleon plate 3 with stout posterior tooth or hook; peraeopod 7, hind margin of basis with 5-10 distinct serrations; telson lobes each about twice as long as wide 2.
—Pleon plate 3 squarish or rounded behind; peraeopod 7, hind margin of basis with small or indistinct teeth of with one large process telson lobes about three times as long as wide 4.
2. Pleon plate 3, tooth heavy rounded; antenna 2, peduncular segments 4 & 5 with single groups of stout facial spines *E. robusta* group 3.
—Pleon plate 3 short, acute; antenna 2, peduncular segments 4 & 5 lacking facial spines
. *E. ochotica* (Gurj.) (p. 92)
3. Peraeopod 7 (male), segment 5 with distinct notch and anterior clasping spine; antenna 2, peduncle 5 with 6-7 anterior marginal calceoli; animals large (12-15 mm) *Eyakia* species 2 (p. 90)
—Peraeopod 7 (male), segment 5 with weak anterior notch and no clasping spine; antenna 2, peduncle 5 with 2-5 anterior marginal calceoli; animals medium (9-11 mm) *E. robusta* (Holmes)(p. 86)

Animals small (6.5 mm) *E. laperousi* (Gurjanova)
4. Peraeopod 7 segment 2 lacks large spike; uropod 2 at least one ramus with marginal spines 5.
—Peraeopod 7, segment 2 with large posterior spike; uropod 2, rami lacking marginal spines 6.
5. Antenna 2 (male), peduncular segment 5 with 4 anterior marginal calceoli; pleon plate 3 rounded behind; peraeopod 7 (male) with strong notch and copulatory spine *E. calcaratus* (Gurj.)(p. 90)
—Antenna 2 (male), peduncular segment 5 with 5-7 anterior marginal calceoli; pleon plate 3 subsquarish, peraeopod 7 (male), segment 5 with weak anterior marginal notch and no copulatory spine
. *Eyakia* species 1 (p. 89)
6. Coxa 2 with postero-ventral tooth; uropod 1, outer ramus with marginal spine(s)
. *E. subuncigera* (Kudrjasch.) (p. 92)
—Coxa 2 lacking postero-ventral tooth; outer ramus of uropod 1 lacking marginal spines
. *E. uncigera* (Gurj.) (p. 92)

toothed pleon plate 3, strongly setose coxal plates 1-4, and relatively short, broad, telson lobes. At least two species occur on both coasts. The *calcaratus* group is mainly Asiatic Pacific. Member species lack a pleonal tooth, the coxal plates are less strongly setose below, and the telson lobes are relatively long and slender. *Eyakia laperousi* is removed from the genus *Mesophoxus*, on the logical recommendation of Barnard & Karaman (1991: 621).

Eyakia robusta (Holmes)
(Figs. 8, 9)

Paraphoxus robustus Holmes, 1908: 518, fig. 27.—Barnard, 1960: 235, pl. 25.
Eyakia robusta: Barnard & Barnard, 1981: 309 (partim).—Barnard & Karaman, 1991: 609.

Material Examined:

BRITISH COLUMBIA: North Central coast: Swanson Bay, C. Levings coll., Nov., 1978 - 2 specimens.
Southern Vancouver I., Saturna I., J.F.L. Hart coll., Aug. 24, 1955: 1 female ov. (9.0 mm), with slide mount. CMN Cat. No. NMCC1992-0999 (fig'd); 1 male (7.0 mm), with

slide mount, CMN Cat No. NMCC1992-0999 (fig'd).
French Creek, P. O'Rourke coll., August, 1977 - 1 female;
Saanich Inlet, 3 stations, K. E. Conlan, August, 1977-4 females ov., with 1 slide mount.

Victoria region: Off Clover Point, G. O'Connell, 1982 - 1 female.

WASHINGTON: Strait of Juan de Fuca, 3 localities, C. P. Staude coll., May, 1976 - 3 females, 2 im.

Diagnosis. Female (9.0 mm): Rostrum medium. Eye small, oval. Antenna 1, peduncular segment 2 with postero-distal cluster of 7-8 setae; flagellum 10-12 segmented, accessory flagellum 7-segmented. Antenna 2, peduncular segment 4 with anterior marginal cluster of 6-8 strong setae and 2 facial clusters of 2-5 spines; segment 5 with central facial cluster of 3 spines and distal group of 2-3 spines; flagellum 10-segmented.

Mandibular molar, apex flat, not triturative, with single movable serrated blade and seta; right lacinia irregularly bifid; spine row with 8-12 serrated blades, left lacinia 4-

FIG. 8. *Eyakia robusta* (Holmes 1908).
FEMALE (9.0 mm) HOLOTYPE; MALE (7.0 mm)
ALLOTYPE (SEE PAGE 87 - OPPOSITE)



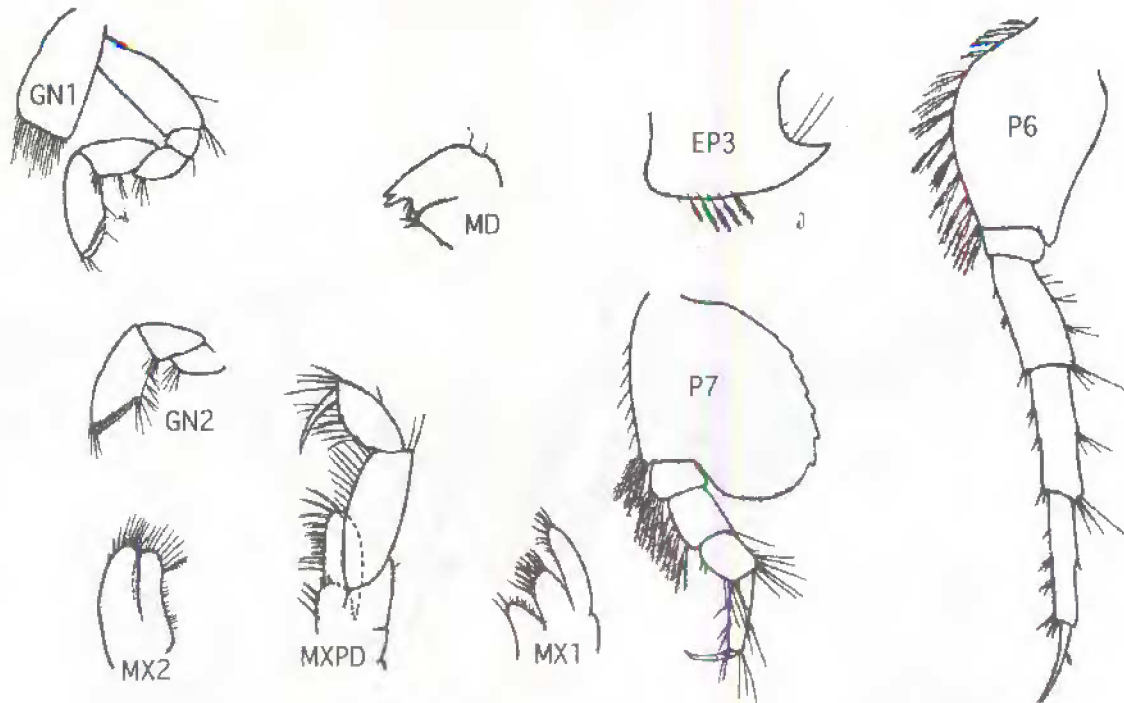


FIG. 9. *Eyakia robusta* (Holmes) ♀ (8.0 mm). off Point Loma, CA.
(modified from Holmes, 1908).

dentate; palp segment 3 with baso-facial cluster of 4-5 medium setae. Maxilla 1, inner plate with 2 apical setae, bluntly conical apex of palp with 4-5 spines. Maxilliped outer plate tall, with 4-5 strong apical spines, and 2-3 outer marginal setae.

Coxal plate 1, lower margin with ~ 20 long setae, corners rounded. Coxa 4 broad, hind margin vertical. Gnathopod propods subequal, ordinary. Gnathopod 1, carpus nearly as long as propod, lower margin with 2 clusters of setae. Gnathopod 2, carpus short, free lower margin with single setal cluster. Pereopods 3 & 4, postero-distal spine of segment 5 stout, length nearly equal to segment 6; posterior margin of segment 6, distal half spinose; dactyl strong, > half length of segment 6. Pereopod 5, segments 4 & 5 little expanded, margins heavily setose, segments 5 & 6 subequal in length, dactyl short. Pereopod 6, segment 4 slightly wider than 5, hind margins long-setose. Pereopod 7, hind margin of basis with 8 medium teeth; segments 4 & 5 slightly expanded, as wide as long, margins strongly setose; dactyl medium.

Pleon plate 3, hind corner produced as strong tooth; facial row of 18-20 long setae; lower margin with 5 plumose setae. Uropod 1, peduncle with baso-facial fan of 10 setae; rami each with 2 closely set marginal spines. Uropod 2, peduncular outer margin with 12-15 tall spines, rami with 2-3 close-set marginal spines. Uropod 3, peduncular distal fan of spines strong; outer ramus twice length of inner ramus, inner distal margin setose, terminal segment short.

Telson lobes, length about twice width, apex with 2 unequal spines.

Male (7.0 mm): Eye large, irregular. Antenna 1, single calceolus on peduncular segment 3 and on proximal 3 of 10 flagellar segments. Antenna 2, peduncular segment 4 with 3 facial clusters of spines; segment 5 with one cluster of facial spines and 5 anterior marginal calceoli; flagellum 30+ segmented; proximal 9 segments with calceoli.

Pereopod 7, copulatory apparatus of segment 5 consists of a slightly emarginated anterior border lined with short spines but none specialized as a copulatory spine.

Uropod 3, rami broadly lanceolate, subequal; all margins setose; terminal segment of outer ramus very small.

Distributional Commentary: *Eyakia robusta* (Holmes, sens. str.) has now been recorded from central and southern British Columbia to southern California, in shelf waters to depths of 20 - 250 m.

Taxonomic Commentary: Except for its slightly larger size, the present material compares closely with that originally described from southern California by Holmes (1908) and redescribed and figured by Barnard (1960) (fig. 9, above). It differs significantly from the large species from the Aleutian Islands described by Barnard and Barnard (1981, fig. 1) by the characters given in the key (p. 86).

This male of this large unnamed species has a very distinctive copulatory spine on pereopod 7 (see fig. 10A), and more closely resembling that of *E. calacurata* (fig. 11).

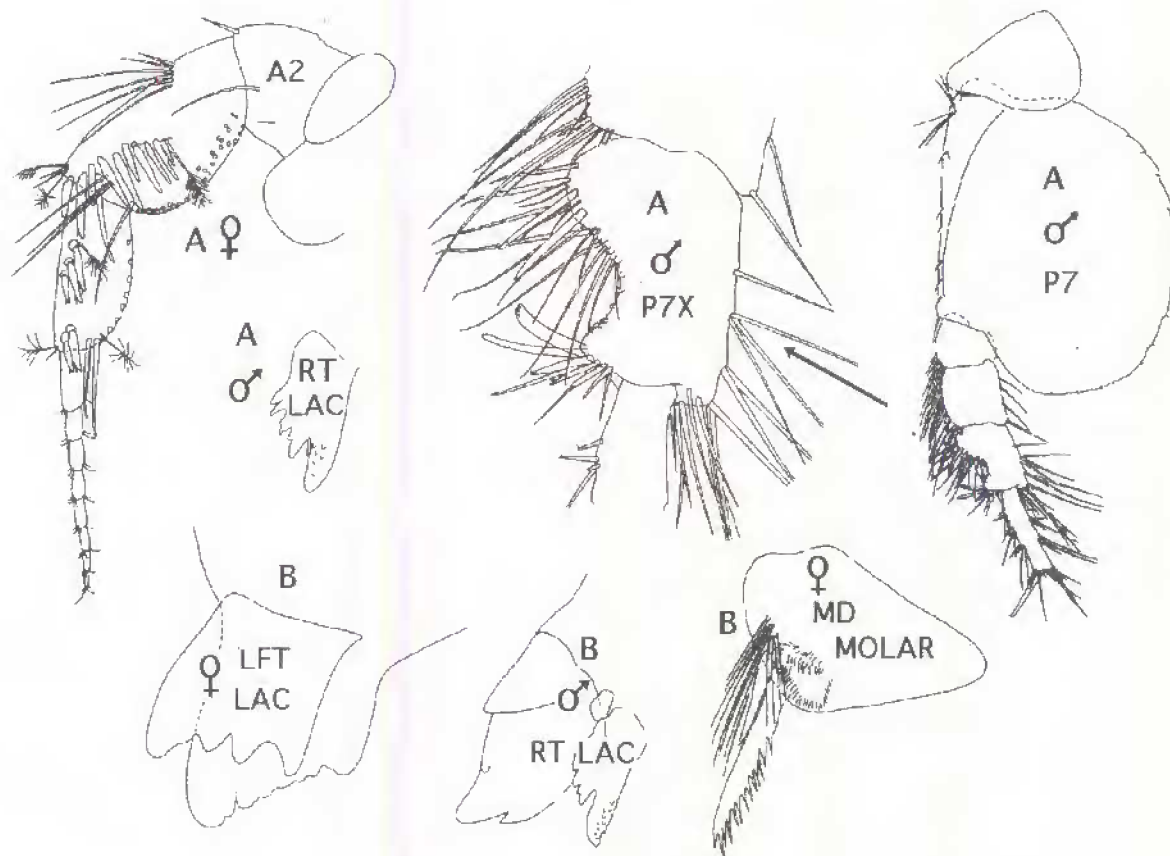


FIG. 10. SPECIES OF *EYAKIA* (AFTER BARNARD & BARNARD, 1981)

A. - *Eyakia* species 1. Male (12.0 mm); Female (15.0 mm) Adakh I.
 B. - *Eyakia robusta* (Holmes)?

Eyakia species 1
 (Fig. 10A)

Eyakia robusta J. L. and C. M. Barnard, 1981: 305, fig. 1.

Material Examined: No specimens of this species were identified in the present extensive phoxocephalid material from the Aleutians to Washington and Oregon states.

The description and figures of Barnard and Barnard apply to a large male "m" (12.0 mm) and a larger female "y" (15.0 mm), from an "Albatross" Stn. off. Adakh Island, Alaska, July, 1893, surface. Other material from Alaska is listed by Barnard & Barnard (loc. cit.).

Diagnosis: Female (15.0 mm): Antenna 2, peduncular segment 2 with 2 weakly separated facial clusters of heavy spines; segment 5 with a single median facial cluster of 3 spines and a terminal cluster of 2 spines.

Male (12.0 mm). The copulatory apparatus of peraeopod 7 differs markedly from that rediagnosed for *E. robusta* (p. 87). Anterior margin of segment 5 deeply and broadly, lower corner subacute, with a fan of stout spines, the largest of which is much thicker than the others, is slightly curved upwards, and has a striated apex. The excavated margin is

lined with very short blunt spines and some longish setae. The basis of peraeopod 7 is much deeper and less broad, and the 8-10 teeth of the posterior margin are low and barely discernible.

Distribution: Barnard & Barnard (loc. cit.) list material from the inner Aleutian Islands, through Prince William Sound and SE Alaska to Friday Harbor, Washington. Their material from Bahia de San Quintin, Baja California, Mexico, is referable to *E. robusta* (Holmes).

Taxonomic commentary: This large species from southern Bering Sea and SE Alaska differs from *E. robusta* (Holmes) by the characters given in the key and by the following. Especially significant in the male is the deeply concave anterior marginal notch, and short copulatory spine of segment 5 of peraeopod 7, and in the female, the short peduncular segment 2 of antenna 1.

The Barnardian description (1981, p. 305, fig. 1) of female "w" (9.12 mm) from VELERO IV Stations, southern California, applies reasonably closely to Holme's TYPE 8.0 mm female of *E. robusta* from off Pt. Loma, CA. (Fig. 10B, above).

Eyakia calcarata (Gurjanova)
(Fig. 11)

Parharpinia calcarata Gurjanova, 1938: 271, figs. 9a-b.—
Gurjanova, 1951: 388, figs 237 A, V, B.
non *Paraphoxus calcaratus* Barnard, 1960: 238, pl. 26.—
non *Eyakia calcarata* Barnard & Barnard, 1981: 309.

Material Examined: The species apparently occurs in the Bering Sea region, and might be anticipated from the study area. However, no specimens were identified in the present material.

Diagnosis. (Male, 12.0 mm): Rostrum long, reaching to end of antenna 1, peduncular segment 2. Eye very large, regular. Antenna 1, peduncle 2, posterior margin with cluster of 6 setae; single calceolus on each of proximal 4 segments of 10-segmented flagellum. Antenna 2, peduncular segment 4 with 3 facial clusters of 3-5 spines; segment 5 with single facial cluster of 4 spines, and 7 anterior marginal calceoli.

Mandible, spine row of 8 blades; palp segment 3 with baso-facial fan of 4 unequal setae. Maxilla 1, palp apically truncate with 6-8 spines. Maxilliped, outer plate with 6-7 long subapical spines and 4-5 strong outer marginal setae.

Coxa 1, lower margin with about 15 long setae, hind corner subacute. Coxa 4 relatively narrow, hind margin steeply oblique. Gnathopod propods subsimilar. Gnathopod 1, carpus as long as propod, lower margin with 3-4 clusters of setae.

Peraeopods 3 & 4, hind margin of segment 6 apparently lacking distal spines; dactyl stout, half length of segment 6. Peraeopod 6, basis little broadened, hind margin straight; segments 4-6 slender, margins not strongly setose or spinose; dactyl large. Peraeopod 7, basis broadly rounded, hind margin nearly smooth; copulatory apparatus of segment 5 very distinctive: anterior margin deeply and narrowly notched, with one large, apically striated, upward-curving spine inserted at lower corner.

Pleon plate 3, hind corner subtruncate; facial row of about 18 medium setae, and lower margin with 6 setae. Uropod 2, outer margin with 9 tall slender spines; outer ramus with 5 close-set spines, inner ramus bare. Uropod 3, peduncular fan of 10 stout spines; outer ramus slightly the shorter, all margins densely plumose-setose.

Telson lobes slender, length 3X width, apex with 2 very unequal slender spines.

Distributional Ecology: Taken near Vladivostok, Russian coast of the Sea of Japan, in depths to 75 m.

Taxonomic Commentary: The female of this species from the type locality has yet to be described. The species is quite distinct from that from southern California identified under this name by Barnard (loc. cit.).

Eyakia species 2

Paraphoxus calcarata Barnard, 1960: 238, plate 26.
Eyakia calcarata Barnard & Barnard, 1981: 309.
non *Parharpinia calcarata* Gurjanova, 1938: 271.

Material Examined: This southern Californian species, originally identified as *E. calcarata* by J. L. Barnard (1960), was not detected in the present material from Alaska to northern California. A brief rediagnosis of Barnard's female (9.0 mm) from AHF Stn. 1156-40, San Pedro Basin, off S. California, reveals important differences from Gurjanova's species, here also rediagnosed and refigured (above). A male (6.0 mm) from AHF Stn. 201-34, and some 16 other specimens taken at 8 stations of that survey, await re-examination and full rediagnosis.

Diagnosis. Female (9.0 mm): The following features differ from *E. calcarata*, as figured by Gurjanova, 1951:

Rostrum medium, not reaching tip of peduncular segment 2 of antenna 1. Eye medium small. Antenna 2, peduncular segment 4 with single distal row of stout facial spines; segment 5 lacking facial spines.

Mandible, palp segment 3 with 3-4 baso-facial setae.

Coxa 1, lower margin with about 10 long setae. Coxa 4 broad, margins rounded, not squared. Gnathopod 1, carpus shorter than propod, weakly setose below.

Peraeopods 3 & 4, distal segment slender, segment 6 lacking posterior marginal spines. Peraeopod 5, segments 4 & 5 little expanded. Peraeopod 7, basis, hind margin with about 4 small but distinct teeth.

Pleon plate 3, hind corner rounded, not squared. Uropod 3, inner ramus very short, < 1/3 outer ramus; terminal segment relatively large, 1/4 length of proximal segment.

Telson lobes very long relative to width ($L > 3X$ width).

Male (7.5 mm): Eyes large, subrotund, nearly meeting mid-dorsally. Antenna 2, peduncular segment 4 with distal facial row of 4-5 spines; segment 5 with 2 slender facial spines. Copulatory apparatus of peraeopod 7 not described. Uropod 3, rami less setose than in *E. calcarata*.

Taxonomic and Distributional Commentary: Barnard's material was taken on the east side of San Pedro Basin and the western slope of Santa Monica Basin at depths to 380 m.

Material from the Galapagos Islands (Barnadian female "n" (6.41 mm), and other material from off Gorgona island, Columbia, is probably referable to different, yet undescribed, species.

FIG. 11. *Eyakia calcarata* (Gurjanova, 1938).
MALE (12.0 mm) HOLOTYPE
(SEE PAGE 91 - OPPOSITE)

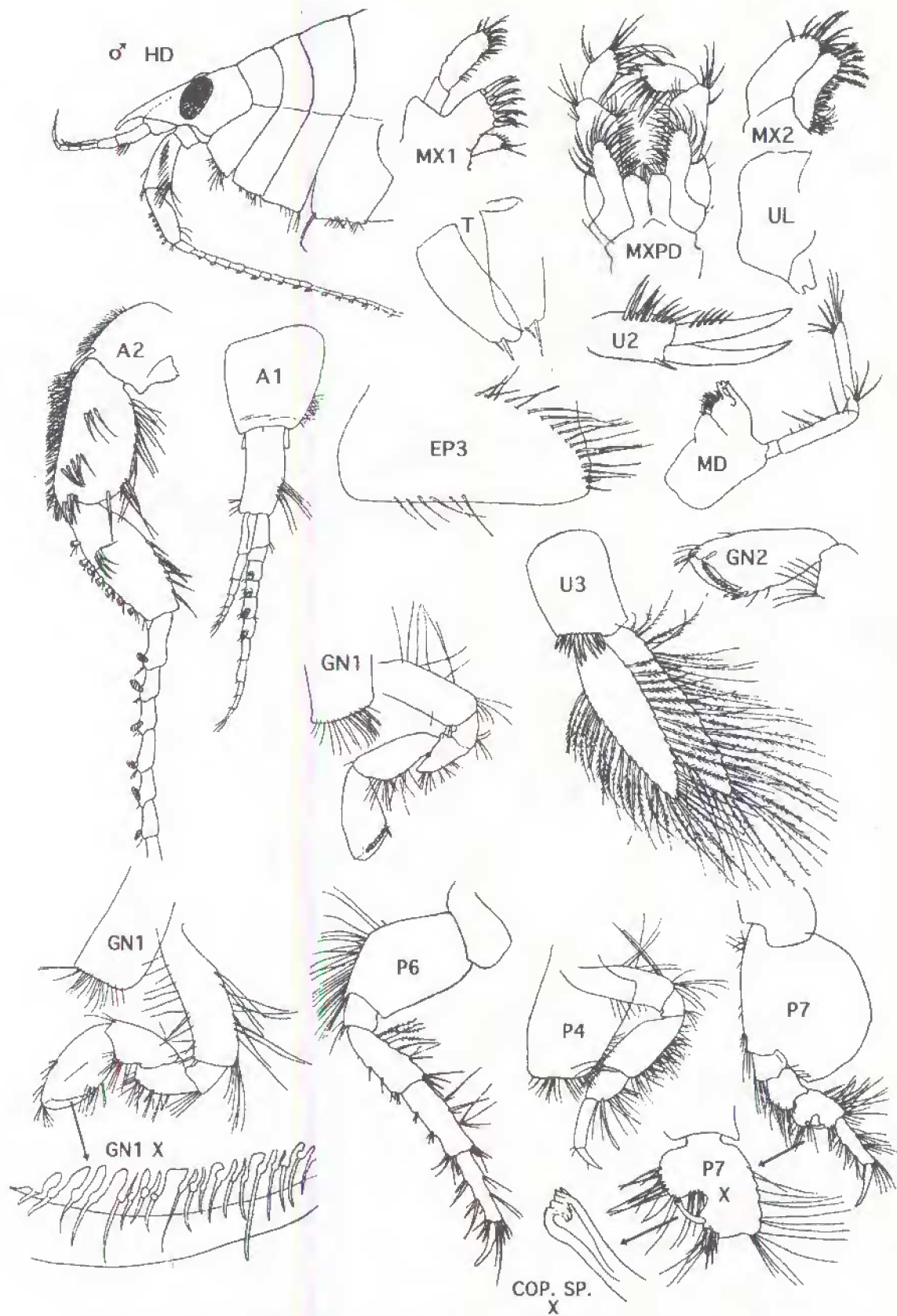


FIG. 11. *Eyakia calcarata* (Gurjanova). ♂ (12.0 mm) Japan Sea.
(modified from Gurjanova, 1951).

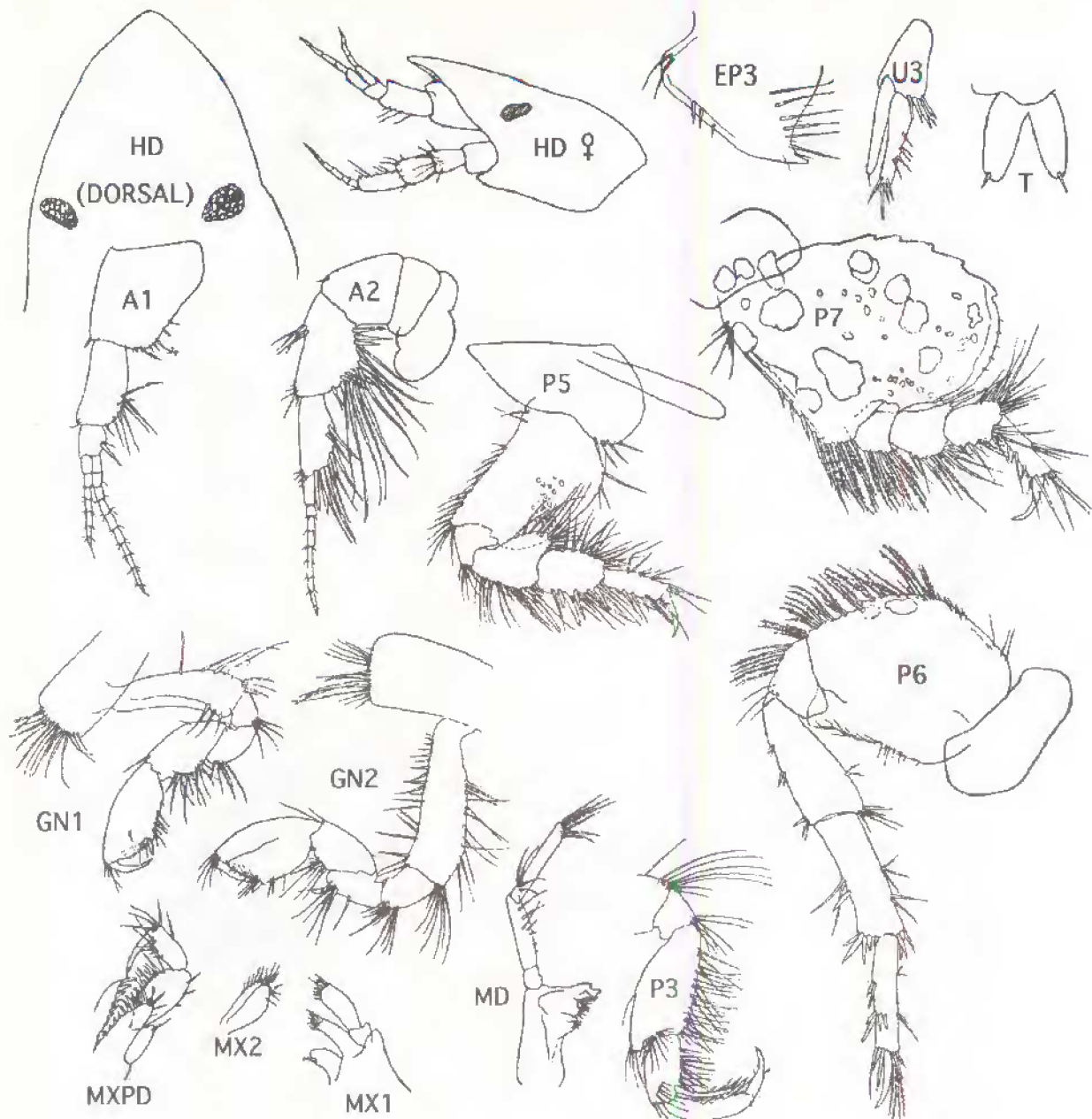


FIG. 12. *Eyakia ochotica* (Gurjanova). ♀ (7.0 mm). Okhotsk Sea (modified from Gurjanova, 1951).

Extralimital Species of *Eyakia*

Three other species of *Eyakia* from the sea of Okhotsk and far eastern Soviet waters are included in the key here (p. 86) but were not identified in present material from the Bering Sea region. One of these, *E. ochotica* Gurjanova, 1953, is reasonably well diagnosed and figured by that author (Fig. 12). It resembles *E. robusta* in possessing a toothed pleon plate 3, but the tooth is small, and the facial setae are few (6-7). Antenna 1, peduncular segments 4 & 5, apparently lack clusters of facial spines, but the hind margins are richly spinose and setose. Pereopods 3 & 4 are robust, with strong distal spine, and posteriorly spinose segment 6.

In pereopod 5, segment 4 is broadened distally and is distinctly wider than segment 5. In pereopod 7, the basis is extended posteriorly, with about 5 distinct posterior marginal teeth. The gnathopod propods are somewhat dissimilar in form although similar in size.

Two other small species, clearly referable to the genus *Eyakia*, *E. uncigera* and *E. subuncigera*, were described from the Sea of Okhotsk by Gurjanova (1938), but have seldom been recorded since. The morphology of these small species departs markedly from that of previous species in having weakly or sparsely armed coxae, pereopods, and uropods, and the basis of pereopod 7 is produced posteriorly as a large tooth or process.

Brolginae Barnard & Drummond

Brolginae Barnard & Drummond, 1978: 87-89; Barnard & Karaman, 1991: 595 (Key).

Type Genus: *Brolgus* Barnard & Drummond, 1978: 96.

Genera: (N. American Pacific):

Paraphoxus G. O. Sars, 1895: 148 (part).

Eobrolgus J. L. Barnard, 1979: 376.—J.L. Barnard and C. M. Barnard, 1981: 295.

Paramesophoxus Gurjanova, 1977: 76.

Diagnosis: Body regular. Rostrum well developed, hood-like, lacking lateral incisions. Antenna 1, segment 2 short, little longer than 3, segments of accessory flagellum and flagellum transversely separated; in male, basal segments calceolate or callynophorate (conjoint, with strong posterior cluster of long aesthetascs). Antenna 2, peduncular segments 4 & 5 short to medium but not strongly expanded or heavily spinose behind; in male, segments 3 & 4 with anterior marginal brush setae, segment 5 with 2 anterior submarginal calceoli, flagellum elongate, often calceolate on alternate segments.

Mandibular molar non-tritulative, bearing 3 or fewer tightly clumped apical spines; left lacinia 5-6 dentate; right lacinia small or vestigial; blades strong; palp slender, segment 3 usually with "A"-setae. Maxilla 1, outer plate with 9-11 apical spines, inner plate with 1 apical seta. Maxilla 2, inner plate small. Maxilliped, inner and outer plates short, outer with stout inner marginal raptorial spines, palp ordinary, inner margins lacking stout spines.

Coxae 1-4 broad, deep, lower margin setose posteriorly. Gnathopods strongly subchelate, unequal; Gnathopod 1, propod more slender, but carpus longer than in gnathopod 2.

Peraeopods 3 & 4, segments 4 & 5 stout, 6 slender, not spatulate, weakly armed; dactyls normal. Peraeopod 5, basis and segments 4 & 5 expanded behind. Peraeopod 5, segments 4, 5, & 6, slender or little expanded, usually elongate. Peraeopod 7, basis normally expanded posteriorly, lower margin exceeded fully by segment 5, in which (male) the postero-distal copulating spines are weak or lacking.

Pleon plate 3 subquadrate, hind corner not produced, lower margin lacking long marginal and submarginal setae. Pleopod peduncles slightly broadened. Uropods 1 & 2 short, peduncle with disto-lateral and usually medio-lateral spine(s); rami subequal, each with single apical spine. Uropod 3, inner ramus variable, strong, larger and more strongly plumose-setose in male than in female.

Telson lobes narrow, each with single subapical spine.

Coxal gills large, plate-like on peraeopods 2-6, medium small, sac-like on peraeopod 7. Brood plates, small, narrow.

Taxonomic Remarks: The genus *Mandibulophoxus* is here transferred from Brolginae (in which it was initially placed by Barnard and Drummond (*loc. cit.*), to the Pont-

harpiiniinae with which it agrees in nearly all principal character states (see p. 75). Members of family Brolginae are closely related to the Phoxocephalinae in general form of rostrum, antennae, and uropods, but retain a 2-segmented palp in maxilla 1. This feature may be considered convergent, but other differences in the peraeopods and uropod 3 justify retention of the two groups as separate subfamily entities. The genus *Paramesophoxus* Gurjanova is hereby transferred from Phoxocephalinae to Eobrolginae because of eobrolgin characteristics of the male copulatory apparatus

Eobrolgus J. L. Barnard

Eobrolgus Barnard, 1979: 376.—Barnard & Barnard, 1981: 295.—Barnard & Karaman, 1991: 607.

Type species. *Paraphoxus spinosus* Holmes, 1905.

Species: (North Pacific region): *Eobrolgus chumashi* J. L. & C. M. Barnard, 1981: 301, Fig. 1e; *E. pontarpioides* (Gurjanova, 1953): 286, Fig. 15.

Diagnosis (per Barnard & Karaman, 1991: 607). Eyes pigmented (both sexes). Antenna 1, segments of flagellum and accessory flagellum not strongly oblique. Antenna 2, peduncular segment 1 not ensiform; segment 4 with 2+ strong facial rows of thick spines; in male, peduncular segment 5 with 1 antero-distal calceolus (Barnard 1960, pl. 29-2), flagellar segments alternately calceolate.

Mouthparts regular. Mandibular molar medium, with 4+ marginal spines; blade spines prominent; left incisor 5-dentate? Maxilla 1, inner plate with 3-4 apical setae. Maxilliped, palp segment 2 lacking outer marginal setae.

Gnathopods medium, somewhat dissimilar, segment 5 of gnathopod 2 much shorter and more cryptic than in gnathopod 1.

Peraeopods 3 & 4 not stoutly developed, segment 6 with short postero-distal armature; dactyls medium. Peraeopod 6 much longer than peraeopod 5, segments 4 & 5 not (or little) broadened. Peraeopod 7 (male) segment 5 posteriorly with paired slender simple copulating spines; segment 6 with distal comb fringe.

Pleon plate 3, hind margin with 1 to several long setae. Uropod 3 (female) inaequiramous, outer ramus weakly setose, terminal segment with paired apical setae.

Telson regular, lobes smooth above.

Taxonomic Remarks: *Eobrolgus* is distinguished from *Paraphoxus* by the multi-spinose mandibular molar, segment 4 of antenna 2 with 2+ rows of thick facial spines; maxilla 1, inner plate with 3+ apical setae; and pleon plate 3 with posterior marginal seta(e). In *Foxiphalus*, segment 1 of antenna 1 is typically weakly ensiform, and segment 6 of peraeopod 7 (male), is armed with a distal fringe.

This taxon appears to link the Eobrolginae to the Metharpiiniinae through its close resemblance to *Foxiphalus*.

KEY TO SPECIES OF *EOBROLGUS* (after Barnard & Barnard 1981)

1. Telson lobes, each with 2 apical spines *E. pontarpinioides* (Gurjanova) (p. 96)
 ---Telson lobes each with one apical spine 2.
2. Pleon plate 3, lower margin lacking setae or spines; outer plate of maxilla 1 with 9 spines
 *E. spinosus* (Holmes)
 --- Pleon plate 3, lower margin with 1-3 setae; maxilla 1, outer plate with 11 apical spines
 *E. chumashi* Barnard & Barnard (p. 94)

Eobrolgus chumashi Barnard & Barnard
 (Fig. 13)

Paraphoxus spinosus J.L. Barnard, 1960: 243 pl. 29 (partim).
Eobrolgus chumashi J. L. and C. M. Barnard, 1981: 301 (part).—J.L. and C.M. Barnard, 1982a: 370 (partim).

Material Examined: ALASKA: Amchitka I., Banjo Point, C.E.O'Clair: 8 specimens; S.E. Alaska, June-July, 1961, ELB Stns. A19(1); A30 (25); A33(30), July, 1980, ELB Stn. S13B1 (2).

BRITISH COLUMBIA: Queen Charlotte Islands, ELB Stns. E25 (1); H4a(1); H8(a & b) (15 specimens including 1 female ov (3.5 mm); H9 (15 specimens including 1 male (3.5 mm); H14 (10).

North Central coast: ELB Stns, 1964: H13 (3); H39 (1). ELB Stns., 1964: H10 (several, including female (3.5 mm) variant.

Vancouver Island: ELB Stns, 1955: F9 (1); ELB Stns. 1970: P710 (14); P711 (1); P715 (c 100); P716 (c 200); P717 (c. 200); P721 (15). ELB Stns., 1976: B5 (1); B11b (6); ELB Stns., 1977: B5a (50 specimens, including 1 male (3.5 mm)); B6a (2); B6b (30); B7a (1); B7b (20); B11b (2). Shoal Bay, J. F. L. Hart, 1935: 1 specimen. Discovery Passage, R. Rafi coll., Aug. 21-23, 1984: about 90 males and females, including 1 female ov (3.5 mm), slide mount, and 1 male (3.0 mm), + slide mount CMN Cat. No. NMCC1992-1115.

WASHINGTON and OREGON: ELB Stns. 1966: W31 (6); W50 (several, including 1 female ov. (4.5 mm); W63 (1). Strait of Juan de Fuca, C. P. Staude colls., 1976: 80 specimens in 9 lots, including 1 female ov. (3.0 mm).

Diagnosis: Female ov. (4.5 mm): Rostrum medium, nearly reaching end of antennal peduncle segment 2, apex obtuse. Eye relative large, oval. Antenna 1, peduncle 2 with strong postero-distal setal cluster; flagellum 6-segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 with 2 major facial clusters of strong spines, anterior margin with cluster of single spine and seta; segment 5 with single distal spine, and medial facial cluster of stout spines; flagellum 8-segmented.

Mandible, apex flat but not triturative, bearing 1 stout spine and 3-4 movable spines, spine row with 8 heavy pectinate blades; left lacinia irregularly 5-dentate, right lacinia bifid; palp segment 5 with 2 medium baso-facial setae. Maxilla 1, inner plate with 2 strong apical setae; outer plate with 11 apical spines; palp 2-segmented, apex subconical, 5-

6 spinose. Maxilliped, outer plate short, apically with 3-4 curved pectinate spines; inner plate with 1 peg spine; palp, dactyl heavy, basally exceeded slightly by segment 3.

Coxa 1 not expanded distally, lower hind corner with 6-8 long setae. Coxa 4 very deep, excavation shallow, hind margin steeply straight. Gnathopods 1 & 2, propods subsimilar; gnathopod 2, carpus with free hind margin and cluster of setae.

Peraeopods 3 & 4 stout, segment 5, distal spine shorter than segment 6, dactyls short. Peraeopod 5, basis broad, hind margin nearly straight; segments 5 & 6 expanded, width greater than depth, margins spinose and setose; dactyl short. Peraeopod 6, basis broadening distally, hind margin straight; segments 4 & 5 little broadened, weakly setose. Peraeopod 7, basis produced postero-ventrally, hind margin rounded, with 4-5 small but distinct teeth, segments 4 & 5 little broadened

Pleon 3, hind corner squarish, hind margin with 3 longish setae, lower margin with 2 slender spines. Uropod 1 peduncle nearly bare, with single baso-facial seta and inner distal displaced spine, rami subequal, each with single marginal spine. Uropod 2, peduncle with 4-5 stout outer marginal spines. Uropod 3 stout, inner ramus very short, terminal segment of outer ramus short.

Telson lobes, length about 2X width, each with single short apical spine.

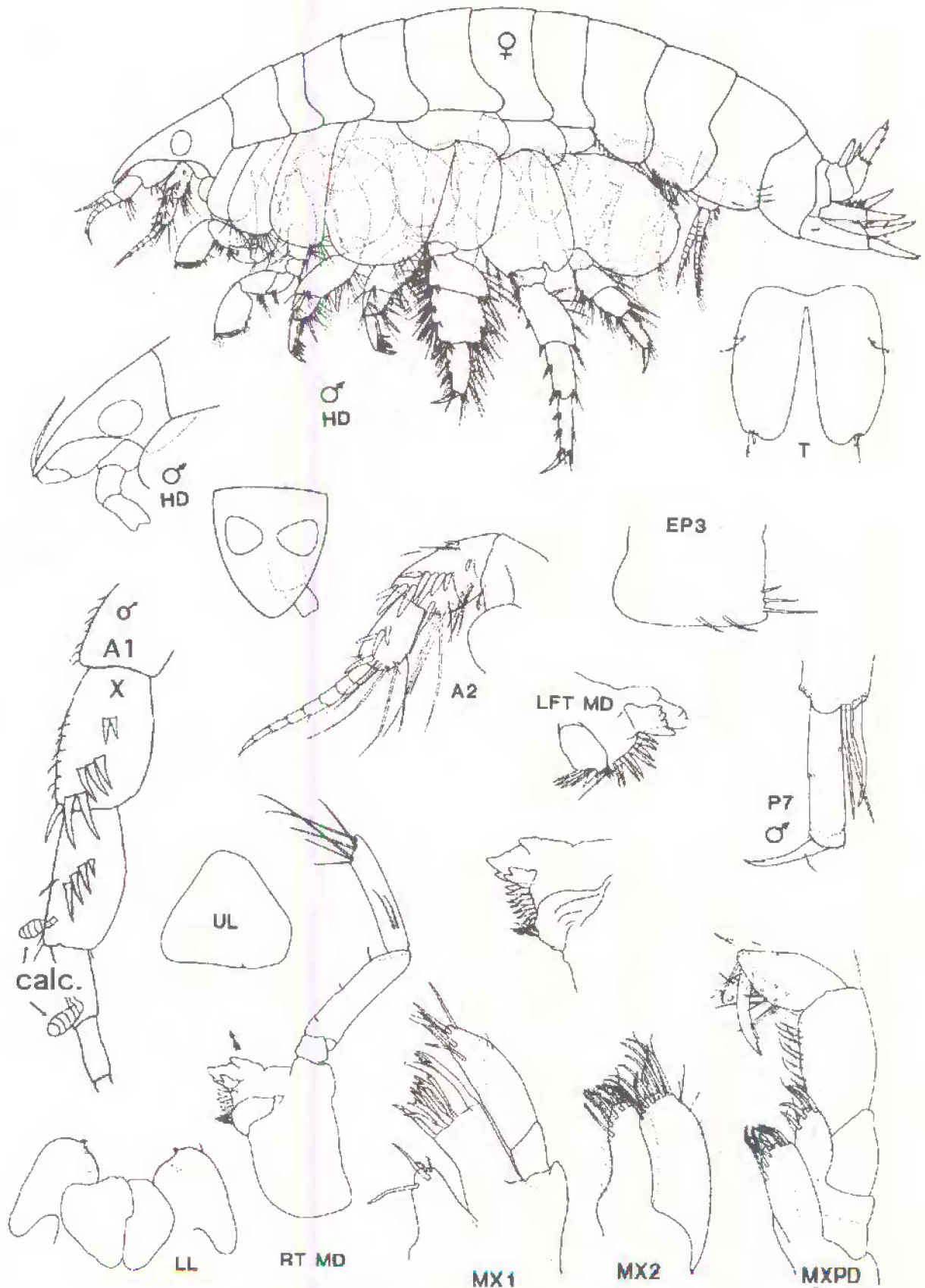
Coxal gills large, plate-like on peraeopods 2-5, smaller on peraeopod 6, small and sac-like on peraeopod 7.

Male (3.0 mm): Eyes large, about twice size of female's. Antenna 1, proximal 3-4 segments of flagellum calceolate. Antenna 2, peduncular segment 3 & 4 with typical anterior marginal brush setae; segment 5 with single antero-distal calceolus; flagellum elongate, alternate segments calceolate.

Peraeopod 7, segment 5 postero-distally with 2 slender pectinate, and one heavy bent, copulatory spines; segment 6 straight, with distal marginal pectinations.

Taxonomic Commentary: This material is identical with that figured from the San Juan Islands, Wash., by Barnard 1960, plate 29. It is distinct from that described and figured as "*P. spinosus*" by Barnard, 1960, pls 30, 31, but reasonably close to "*E. chumashi*" described from Califor-

FIG.13. *Eobrolgus chumasi* Barnard & Barnard.
 FEMALE ov. (3.5 mm); MALE (3.0 mm). Discovery Passage, B.C. (SEE PAGE 95 - OPPOSITE)



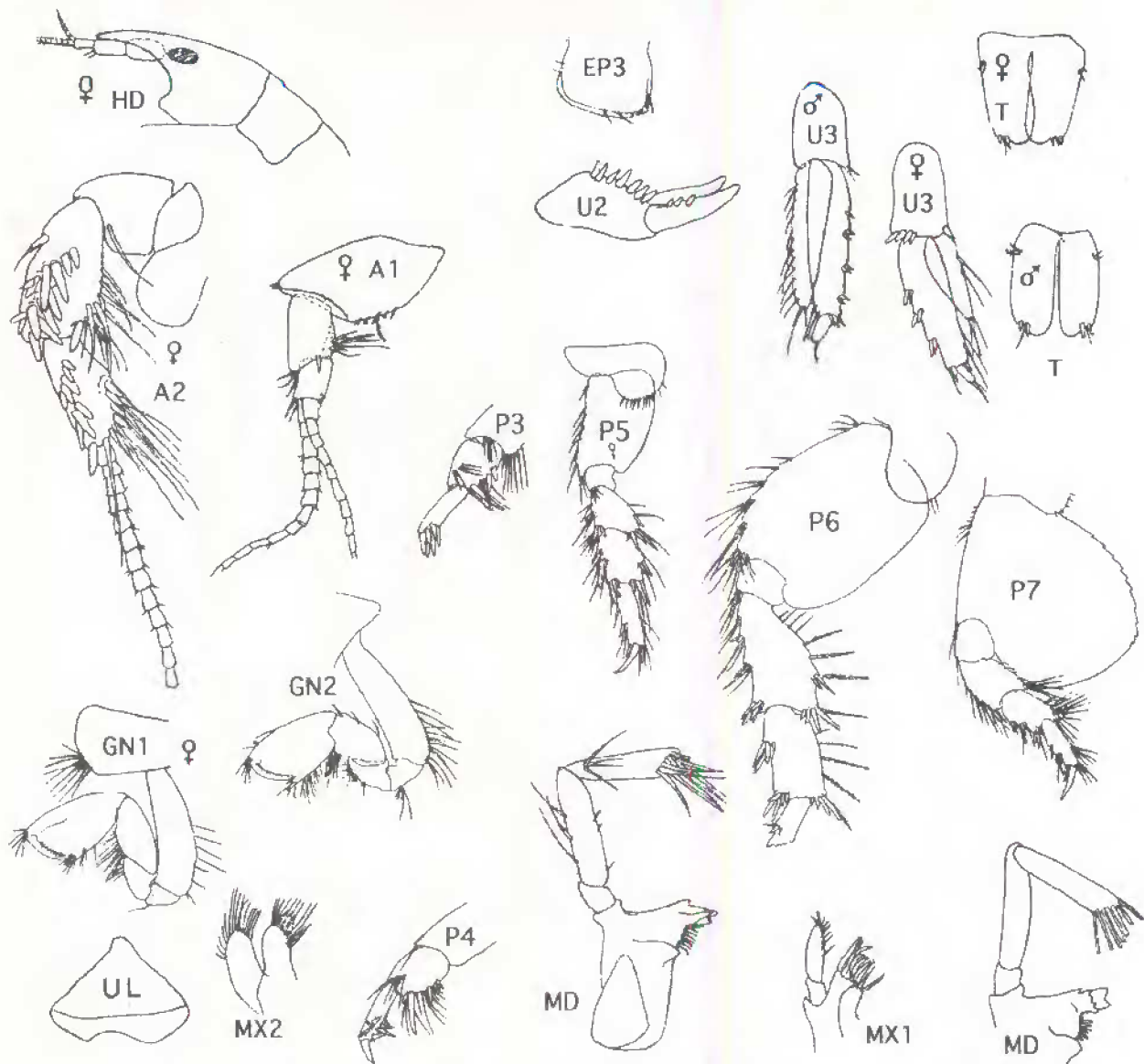


FIG. 14. *Eobrolgus(?) pontarpioides* (Gurjanova). Female (13.0 mm). Kurile Ids. (modified from Gurjanova, 1953, figs. 11 & 12)

nia by Barnard & Barnard (1981, 1982). Barnard's southern material is all "open sea" whereas that from BC is nearly all intertidal, on both outer and inner coasts. B. & B.'s 1982 paper gives the depth range as 0-11 m. We suspect that two or more species may be involved in the northern material, especially that from Oregon. It differs from regular "chumashi" in uropod 1 which apparently has a displaced spine, and in the lobes of the telson which taper distally. Uropod 3 regular, rami subequal and margins setose

The northern material (San Juan Island) figured by Barnard (1960) is identical to the material in collections of this study, described and figured above. This material differs from Barnardian type material from southern California not only in its larger size (4.5 mm vs. 2.5 mm), but also in the more acutely pointed rostrum, narrower and deeper coxa 4; shorter stouter segments and dactyl of pereopod 6, and more setose anterior margins of pereopod 7, segments 4 & 5.

Distributional Commentary: North Pacific species of *Eobrolgus* form a complex extending from the Japan Sea and Kamchatka region, via Alaska and British Columbia, south to southern California. The animals occur essentially in shallow water, near shore, in medium fine sands, often in association with species of *Foxiphalus* and *Rhepoxynius*.

Eobrolgus pontarpioides (Gurjanova)
(Fig. 14)

Pontarpinia pontarpioides Gurjanova, 1953: 229, figs. 11, 12.

Eobrolgus pontarpioides Barnard & Barnard, 1981: 304, + Key—Barnard & Karaman, 1991: 607.

Taxonomic Commentary: This large northwestern Pacific form (female to 13 mm) differs from typical southern Californian material of *E. chumasi* in several character states. The flagellum and accessory flagellum of antenna 1 are long (both 10+ segmented); antenna 2, peduncular segment 5 with 2 clusters of very stout facial spines and 4 strong posterior marginal spines. The mandibular palp has a cluster of 4 baso-facial setae. In gnathopod 2, carpus short, hind margin nearly cryptic. In peraeopod 5, segments 4 & 5 stoutly spinose; in peraeopod 6, segments 4 & 5 somewhat broadened and setose behind; and in peraeopod 7, hind margin with about 10 weak teeth. Pleon plate 3, hind margin with 1 posterior marginal seta. Uropod 2, outer ramus with 3 marginal spines. Uropod 3, inner ramus > 1/2 outer ramus. Telson lobes apically with 3 short spines. Resolution of the taxonomic significance of such differences requires a geographically more extensive series of specimens than available to the authors.

Distribution. Sea of Okhotsk: Kurile Islands, Ekatera I.

Paraphoxus G. O. Sars

Paraphoxus G. O. Sars, 1895: 148.—Gurjanova, 1951: 364.—Barnard, 1969: 420(partim).—Barnard & Drummond, 1976: 524.—Barnard & Drummond, 1978: 144.—Barnard & Karaman, 1991: 625.

non *Paraphoxus* Bousfield, 1973: 124. (= *Eobrolgus*).

Type Species. *Phoxus oculatus* Sars 1879, monotypy. (E. North Atlantic).

Species (North Pacific regional): *Paraphoxus beringiensis*, new species; *P. similis* new species (Bering Sea); *P. simplex* Gurjanova 1938 [272] (Japan Sea); *P. tomiokaensis* Hirayama, 1987 [48], (Japan Inland Sea); *P. gracilis*, new species (B.C. fiords); *P. rugosus* new species (Bering sea); *P. communis*, new species (and variations) (B.C.); *P. pacificus*, new species; *Paraphoxus* sp. 1 (= *P. oculatus* Barnard, 1960 [240] (S. California)); and *Paraphoxus* sp. 2 (= *P. oculatus* Hirayama, 1992 [118] (Hong Kong)).

Diagnosis. (see Barnard & Karaman, 1991: 625): Rostrum fully hooded, not laterally constricted, apex bluntly rounded. Eyes pigmented (both sexes), much larger in male. Antenna 1, flagellum short, 6-9 segmented, proximal 4-5 segments calceolate in male; accessory flagellum 4-5 segmented. Antenna 2, segment 1 not ensiform; peduncle 4 with distal marginal fan of 6-12 stout fossorial spines; segment 5 (male) with 2 antero-distal marginal calceoli; flagellum of female short, 5-8 segmented, of male, elongate (15-30+ segmented), alternate segments calceolate.

Mandibular molar, apex with 2-4 spines; blade row with 5-10 spines, left lacinia 4-dentate; incisor tricusate; palp segment 3 with 0-4 basofacial "A" setae, and 6-8 distal "C"

setae. Maxilla 1, inner plate with 2 apical setae; outer plate basically with 9 or 11 (occ. 10) apical spines; palp 2-segmented (occ. segments fused), spines and/or setae apical. Maxilla 2, plates weakly apically setose, outer plate distinctly the larger. Maxilliped, outer plate narrow, inner margin with 5-9 distally longer curved masticatory spines; inner plate short, apex with plumose setae; palp, dactyl slender, curved.

Coxae 1-4, postero-distal margins variously lined with simple setae; coxa 1 with 5-12 setae. Gnathopods 1 & 2, propods smoothly subchelate, subsimilar in size and form or, gnathopod 1, propod smaller and more slender, carpus longer than in gnathopod 2; basis of gnathopod 1 variously with longish posterior marginal setae.

Peraeopods 3 & 4, postero-distal fossorial spine and/or adjacent spine of segment 5 stout, often equal to (or longer than) segment 6; dactyl variable, often nearly equal in length to segment 6. Peraeopod 5, coxa with deep rounded hind lobe; basis variably broad, hind margin straight or convex; segment 4 slightly expanded and spinose; segment 6 with 1-3 anterior marginal spines and 0-3 posterior marginal setae. Peraeopod 6 elongate, segments 5-6 slender, with variable numbers of marginal spines and setae. Peraeopod 7, basis variously extended posteriorly, hind margin weakly toothed, segment 5 lacking posterior copulatory spine(s).

Pleon plate 3, hind corner variously produced, broadly rounded, lower margin bare, often straight. Pleopods normal, not sexually dimorphic. Uropods 1-2, rami and peduncles subequal in length. Uropod 1, peduncle with baso-facial cluster of 2-5 setae, but lacking distal displaced spine; rami with 0-3 marginal spines. Uropod 2, peduncle, outer margin usually strongly spinose, rami with 0-2 marginal spines. Uropod 3 (female), outer ramus variably much shorter than inner, terminal segment large (1/4-1/2 proximal segment), apex with 2 unequal simple setae; in male, rami large, subequal, margins plumose-setose. Telson longer than wide, lobes longer in male, slightly diverging, apices slightly oblique, each with 1-3 spines, paired penicillate setae about mid-point. Coxal gills large, plate-like on peraeopods 2-6, small, sac-like on peraeopod 7. Brood plates regular.

Distribution: Mainly amphi-North Pacific, in subarctic and boreal coastal shelf waters; two species (including the type species) are known from eastern North Atlantic and Mediterranean coastal regions.

Taxonomic Commentary: North Pacific species apparently form two principal sub-groups, viz: a relatively primitive *oculatus* subgroup and a more advanced *pacificus* subgroup (see key to species (p.98), and also phenogram). The *oculatus* subgroup is characterized by: gnathopods subsimilar in size and form; peraeopod 3 & 4, dactyls long; maxilla 1, outer plate with 11 apical spines; mandible with 8-10 relatively slender blades; uropods 1 & 2, some rami with 2-3 marginal spines; and telson lobes with 2-3 apical spines.

KEY TO NORTH PACIFIC SPECIES OF *PARAPHOXUS* (FEMALES & IMMATURES)

1. Telson lobes each with 1 apical spine 2.
—Telson lobes each with 2(3) apical spines 3.
2. Peraeopod 5, basis rounded behind; peraeopods 3 & 4, segment 5 with postero-distal subequal pair of stout spines *P. simplex* Gurj. (p. 113)
—Peraeopod 5, basis hind margin straight; peraeopods 3 & 4, segment 5 with single stout postero-distal spine *P. beringiensis* n. sp. (p. 114)
3. Coxa 1, lower margin with 12-14 close-set long setae; maxilla 1, outer plate with 9 apical spines . . . 4.
—Coxa 1, lower margin with 6-9 widely spaced long setae; maxilla 1, outer plate with 11 apical spines 7.
4. Pleon plate 3 produced behind; peraeopods 3 & 4, segment 5 with single stout postero-distal spine 5.
—Pleon plate 3 not produced behind; peraeopods 3 & 4, segment 5 with subequal pair of stout distal spines 6.
5. Uropod 1, basal peduncular fan with 3 spines; mandibular palp segment 3 lacking "A" seta; antenna 2, peduncular segment 4 with distal fan of 6-8 stout spines *P. similis* (p. 110)
—Uropod 1, basal peduncular fan with 4-5 short spines; mandibular palp with 1 "A" seta; antenna 2, peduncular segment 4 with distal fan of 10+ stout spines *P. oculatus* Sars (p. 99)
6. Peraeopod 5, segment 5, anterior spines long; mandibular palp segment 3 lacking "A" seta; peraeopods 3 & 4, segment 5 postero-distal paired spines extend beyond segment 6 . . . *P. rugosus* (p. 111)
—Peraeopod 5, segment 5, anterior spines short; mandibular palp 3 with single "A" seta; peraeopods 3 & 4, segment 5 postero-distal paired spines not extending beyond segment 6 . . . *P. pacificus* (p. 107)
7. Peraeopods 3 & 4, segment 5, distal spines long (beyond segment 6); accessory flagellum 4-5 segmented; mandibular palp segment 3 lacking "A" seta 8.
—Peraeopods 3 & 4, segment 5, distal spines short, (not beyond segment 6); accessory flagellum 4-segmented; mandibular palp, segment 3 with single "A" seta 9.
8. Pleon plate 3, hind corner narrowly rounded; gnathopod 1, propod slender, length 2X depth; peraeopod 6, segment 6, anterior margin with setae only *P. gracilis*, n. sp. (p. 107)
—Pleon plate 3, hind corner broadly rounded; gnathopod 1, propod robust, length 1.5 X depth; peraeopod 6, segment 6, anterior margin with paired spines and setae *P. communis*, n. sp. (p. 102)
9. Pleon plate 3 produced behind; peraeopods 3 & 4, segment 5 with 2 subequal postero-distal stout spines; uropod 1, peduncular basal fan with 2 spines, outer ramus with 2 marginal spines; mandibular palp segment 3 with 1 baso-facial seta *Paraphoxus* sp. 1. (p. 99)
—Pleon plate 3 not produced; peraeopods 3 & 4, segment 5 with single postero-distal stout spine; uropod 1, peduncular basal fan of 4 spines, outer ramus with single marginal spine; mandibular palp with 3 baso-facial setae 10.
10. Antenna 1, flagellum 7-8 segmented; propod (GN1), palm vertical . *P. tomiokaensis* Hiray. (p. 104)
—Antenna 1, flagellum 6-segmented; propod, (GN1), palm oblique *Paraphoxus* sp. 2 (p. 102)

The *pacificus* subgroup generally has, in combination: gnathopods somewhat dissimilar in size and/or form; peraeopods 3 & 4, dactyls short; maxilla 1, outer plates with 9 apical spines; mandible with 4-7 short thick blades; uropods

1 & 2, rami usually with 0-1 marginal spines; and telson lobes each with 1-2 apical spines. The distinctions may yet merit formal subgeneric or generic recognition.

Paraphoxus oculatus (G. O. Sars)

(Fig. 15)

Phoxus oculatus Sars, 1879: 441.149, pl. 51.

Paraphoxus oculatus (Sars, 1895: 149, pl. 51.—Gurjanova, 1951: 364.—Karaman, 1972: 91, figs. 25-28.—Barnard & Karaman, 1991: 625.

non *Paraphoxus oculatus* Barnard, 1960: 240, pls. 27, 28.—Bousfield, 1973: 125, pl. 34.1.—Lincoln, 1979: 368, fig. 174.—Hirayama, 1987: 42.—1992: 118, figs. 1-4.

Diagnosis (after Sars, 1895): Female ov. (5.0 mm): Eyes small, rounded. Antenna 1, flagellum 7-segmented, accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 with distal fan of 10-12 stout spines; flagellum 8-segmented.

Mandibular molar with 2 apical spines, blade row of 7-8 spines; palp segments 2 & 3 subequal, segment 3 with 1 (?) facial "A" seta, segment 2 with strong distal, and weak middle, marginal seta. Maxilla 1, outer plate with 11 apical spines; palp 2-segmented (1-segmented in Sars' description, but his illustration shows marginal separation lines). Maxilliped, outer plate with 9-10 stout inner marginal masticatory spines.

Coxal plate 1 with about 14 tightly grouped lower marginal simple setae; coxa 4 broader than deep. Gnathopods 1 & 2, propods stout, closely subequal in size, segment 5 of peraeopod 2 distinctly shorter than in peraeopod 1, with 3-4 posterior setae.

Peraeopods 3 & 4, segment 5 postero-distally with unequal pair of medium spines not exceeding apex of segment 6 that has 4 inner marginal spines; dactyls subequal in length to segment 6. Peraeopod 5, basis relatively broad, hind margin slightly convex; segment 6 with 2 anterior marginal spines and one posterior marginal seta. Peraeopod 6 elongate, segments 5 & 6 moderately spinose with total of about 10 clusters of spines and long setae. Peraeopod 7, hind margin of basis with 12-14 weak teeth, lower margin evenly convex.

Pleon 3 posteriorly produced, hind corner rounded. Uropod 1, baso-facial fan of 4-5 short slender spines; outer ramus equal to peduncle, with 2-3 slender marginal spines, inner ramus with 2 marginal spines. Uropod 2, rami longer than peduncle, with 1-2 marginal spines; peduncle with 4-5 long stout outer marginal spines. Uropod 3, peduncle with weak distal fan of spines; inner ramus slender, > 1/2 proximal segment of outer ramus, terminal segment slender, elongate. Telson lobes each with pair of apical spines and setae.

Male (4.0 mm): Conforming with the generic diagnosis.

Distributional Remarks: North Atlantic region; coastal Norway to northwestern Russia, and south to the Mediterranean (as *P. maculatus*?) in depths of 12-200 m. Not known authentically from the North Pacific region.

Taxonomic Remarks: The material of "*Paraphoxus oculatus*" from S. California (Barnard, 1960 loc cit) is distinct from Sars species, and may be a distinct new species (see p. 99). The small (4.0 mm) species figured as *P. oculatus* Sars by Lincoln, 1979 (loc. cit.), is very distinct from Sars' species in the heavily setose peraeopod 6, weakly setose coxae 1-4, and single spine of the telson lobes, among other features. It may prove to be a species of *Brolgus* or *Eobrolgus*. Hirayama's well illustrated material of "*Paraphoxus oculatus*" from Hong Kong (loc. cit) appears to be a distinct new species, very closely related to *P. tomioakaensis* from Japan (see p. 102). Except for the small body size of his material, the description and figures of Karaman (loc. cit) agree well with those of Sars (1895) and confirm the form and number of the mandibular blades, and segmentation and armature of maxilla 1, as diagnosed above. Karaman has also formally submerged *P. maculatus* Chvereux, 1989, in this species, but further analysis of all previous N. Atlantic material would seem desirable to confirm this decision.

Paraphoxus sp. 1 (Barnard, 1960)

(Fig. 16)

Paraphoxus oculatus Barnard, 1960: 240, pls. 28, 29 (part).—Austin, 1985: 598?—Staude, 1987: 365?

Material Examined: The diagnosis is based on the description and figures of J. L. Barnard (loc. cit). No material was re-examined.

Diagnosis: This small species differs from Sars' nominate species *oculatus* in the following features:

Female 4.75 mm (stns. 2293-53, above); Rostrum relatively short, not reaching antenna 1 peduncular segment 3. Eyes small, almond-shaped. Antenna 1, flagellum 6-segmented, accessory flagellum 4-segmented; Antenna 2, peduncle 4 with distal facial fan of 9 spines; flagellum 7-segmented.

Mandible, molar with 2-3 apical spines, and 6-7 stout blades; palp segment 3 with 1 baso-facial seta. Maxilla 1, outer plate with 11 apical spines; palp distinctly 2-segmented.

Coxal plates weakly setose below; coxa 1 with 7-8 distal marginal setae; coxa 4 wide, strongly rounded behind. Gnathopods, propods subsimilar.

Peraeopods 3 & 4, postero-distal spine heavy, exceeding apex of segment 6; dactyls slender, length about equal to segment 6. Peraeopod 5, basis not very broad, hind margin gently convex; segment 6 with 2 anterior marginal spines and FIG. 15. *Paraphoxus oculatus* (Sars, 1879)

FEMALE (5.0 mm); MALE (4.0 mm). Norway.

(SEE PAGE 100)

FIG. 16. *Paraphoxus* species 1. (Barnard, 1960).

FEMALE (4.75 mm); MALE (4.5 mm). S. California
(SEE PAGE 101)

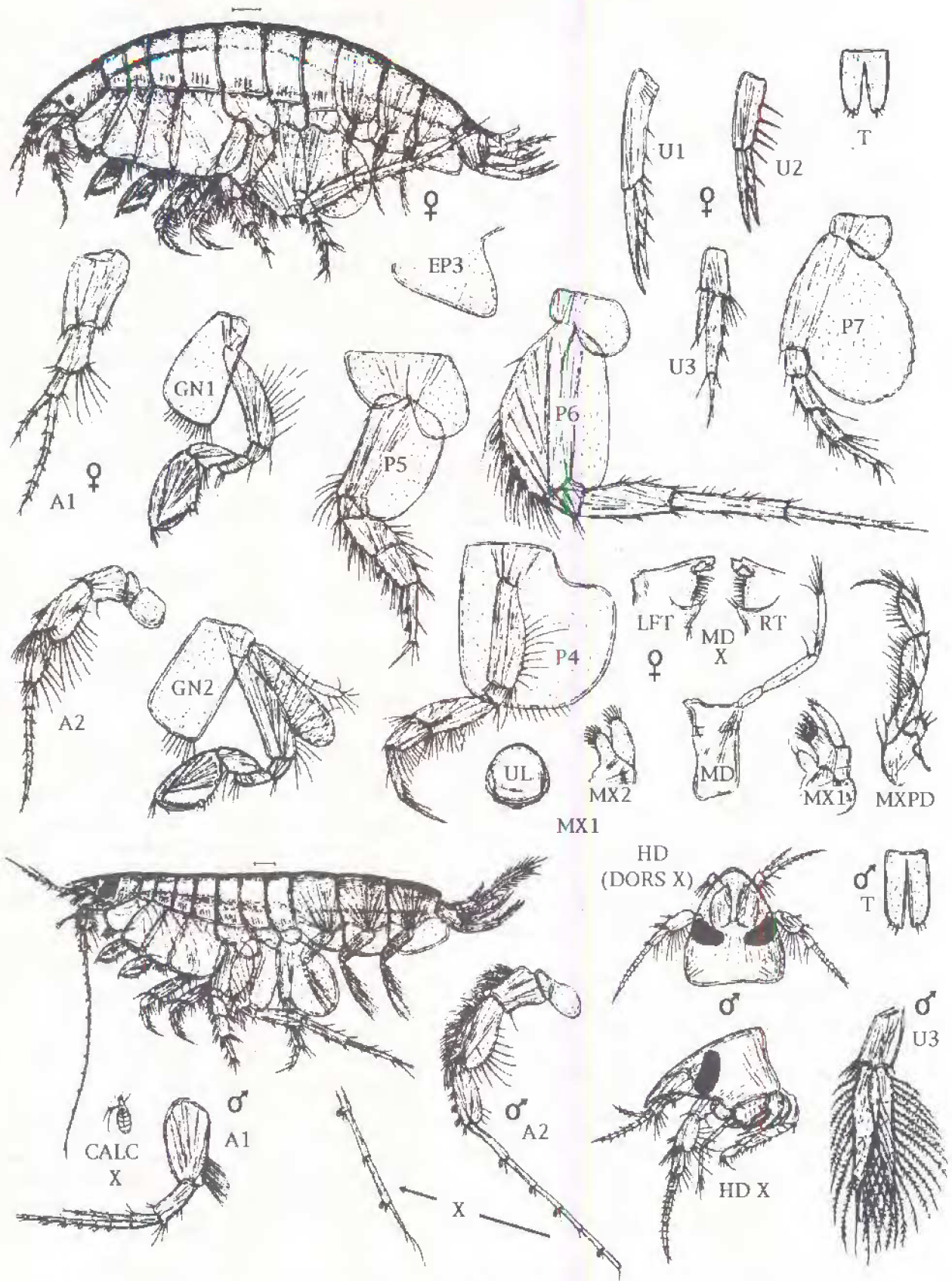


FIG. 15. *Paraphoxus oculatus* Sars ♀ ov. (5.0 mm) ♂ 4.0 mm) Norway (20-100m) (modified from Sars, 1895)

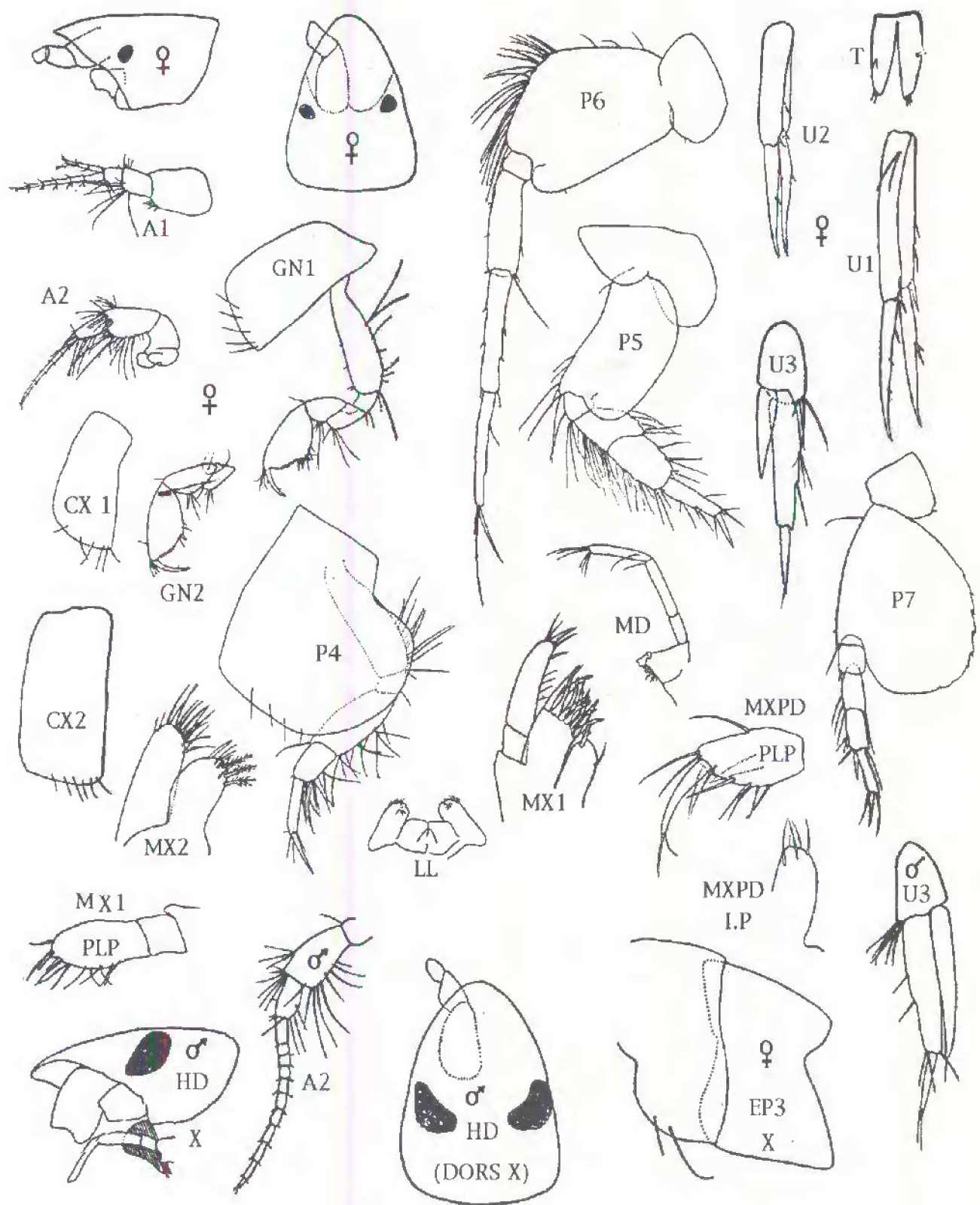


FIG.16. *Paraphoxus* species 1. ♀ ov (4.75 mm) subad ♂ (4.5 mm) S. California (modified from Barnard, 1960)

1 posterior marginal seta. Peraeopod 6 not short, segments 5 & 6 not heavily spinose or setose. Peraeopod 7, basis broad, hind margin with 5-7 small teeth.

Pleon plate 3 produced at hind corner, sharply rounded, lower margin straight. Uropod 1, peduncle with 2 baso-facial setae. Uropods 1 & 2, outer rami with 2-3 marginal spines. Uropod 3, peduncle with distal fan of 5-6 spines; outer ramus 2X inner, terminal segment about 1/2 length of proximal segment.

Male penult (4.5 mm): Eyes medium large, subreniform. Uropod 3, inner ramus equal to basal segment of outer ramus, margins bare.

Adult male not described.

Distribution: Known authentically only from southern California: J. L. Barnard stations in San Pedro and Santa Catalina Basins, and in Santa Monica Bay, 30 - 100 m. Not identified in the present study material.

Taxonomic-Distributional Commentary: The species is similar in most respects to the northeastern Atlantic type species, *P. ocellatus* Sars, but differs in characters of the key, especially in antennal setation and in setation of the coxal plates. It clusters more closely with the North American Pacific coastal *P. gracilis*, and *P. communis* than with counterpart species from the Asiatic Pacific coast. (p. 144). Material from Galapagos Islands, listed under this name by Barnard (*loc. cit.*), is probably also distinct. The material of Staude (*loc. cit.*) was not re-examined but it, and the records of Austin (*loc. cit.*), may be referable, at least in part, to *P. communis* (p. 104).

Paraphoxus species 2.
(Fig. 17)

Paraphoxus ocellatus Hirayama, 1992: 118, figs. 1-5.—
Hirayama, 1987: 48, fig. 253?

Diagnosis: The detailed figures of Hirayama (1992) are utilized here to develop additional diagnostic character states for the key (p. 98) and phenetic analysis (p. 143).

Female ov. (3.2, 3.3 mm). Rostrum short, not attaining segment 3 of antenna 1. Eye small to medium, about 20-faceted. Antenna 1, flagellum 6-segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 with distal facial fan of 8-9 fossorial spines; flagellum of 6-7 segments.

Mandibular molar with 3 thick apical spines; spine row with 5-6 medium blades; palp segment 3 with 3 baso-facial setae. Maxilla 1, outer plate with 11 apical spines, palp 2-segmented. Maxilliped, inner plate distally with 4 large plumose spines.

Coxal plate 1, with 7 lower marginal setae. Coxae 2 & 3, setae posterior only. Coxa 4 deeper than broad, hind margin strongly convex. Gnathopods subsimilar. Gnathopod 1, basis with 3 long posterior marginal setae.

Peraeopods 3 & 4, distal spine of segment 5 heavy, subequal in length to segment 6; dactyl medium long, about 3/4 length of segment 6. Peraeopod 5, basis medium broad, hind margin nearly straight; segment 6 with 2 anterior marginal clusters of spines and 2 posterior marginal stiff setae. Peraeopod 6, segments slender, well armed, marginal spine clusters totalling 13, anterior margin of segment 6 with 2 spine clusters. Peraeopod 7, basis relatively little broadened, hind margin with 8 weak teeth.

Pleon plate 3 not produced, broadly rounded behind, with 1 setule. Uropods 1 & 2, rami with 1-2 marginal spines. Uropod 1, peduncle with 3-4 baso-facial setae. Uropod 3, peduncle with distal fan of 4-5 longish spines; inner ramus very short (< 1/2 outer ramus); terminal segment of outer ramus short, with 2 long apical setae.

Telson, lobes medium, each with 1-2 apical spines.

Distribution: Known from the Hong Kong region of the South China Sea and possibly from the coastal waters of Japan.

Taxonomic Commentary: This species is very close to *P. tomiokaensis* Hirayama from coastal waters of Japan. It differs, however, by characters of the key (above) and by the much more strongly spinose and setose segments 4-6 of peraeopod 6. Material previously recorded from Japan (Tomioka Bay) as *P. ocellatus* (Hirayama, 1987) may also be this species.

Paraphoxus communis, new species
(Fig. 18)

Paraphoxus ocellatus Austin, 1985: 598?—Staude, 1987: 380?

Material Examined:

BRITISH COLUMBIA: Southern Vancouver island: Berkeley Sound, North of Diana Island, ELB Stn. B26, 25-35 m. July 8, 1976. - 1 female Br. III (3.4 mm), with slide mount (fig'd) HOLOTYPE CMN Cat. No. NMCC1992-1123; 1 male penult (3.5 mm) with slide mount (fig'd) ALLOTYPE. CMN Cat. No. NMCC1992-1124; 3 males, penult., with slide mounts, 2 females, with slide mounts, PARATYPES. CMN Cat. No. NMCC1992-1125. plus 51 other females and 36 other male subadults. Off Edward King Island, ELB Stn B28, bed-rock and boulders, *Phyllospadix* community, LW - HW levels, July 10, 1976 - 4 females, 1 male. Off McCauley Point, Victoria, G. W. O'Connell coll., 39 m., Aug. 26, 1976 - 1 female (ov).

Diagnosis: Female (3.4 mm): Rostrum short, reaching little beyond peduncle 1 of antenna 1. Eye small, almond-shaped. Antenna 1, flagellum 6-segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 with distal facial fan of 8-10 slender spines; flagellum 6-segmented.

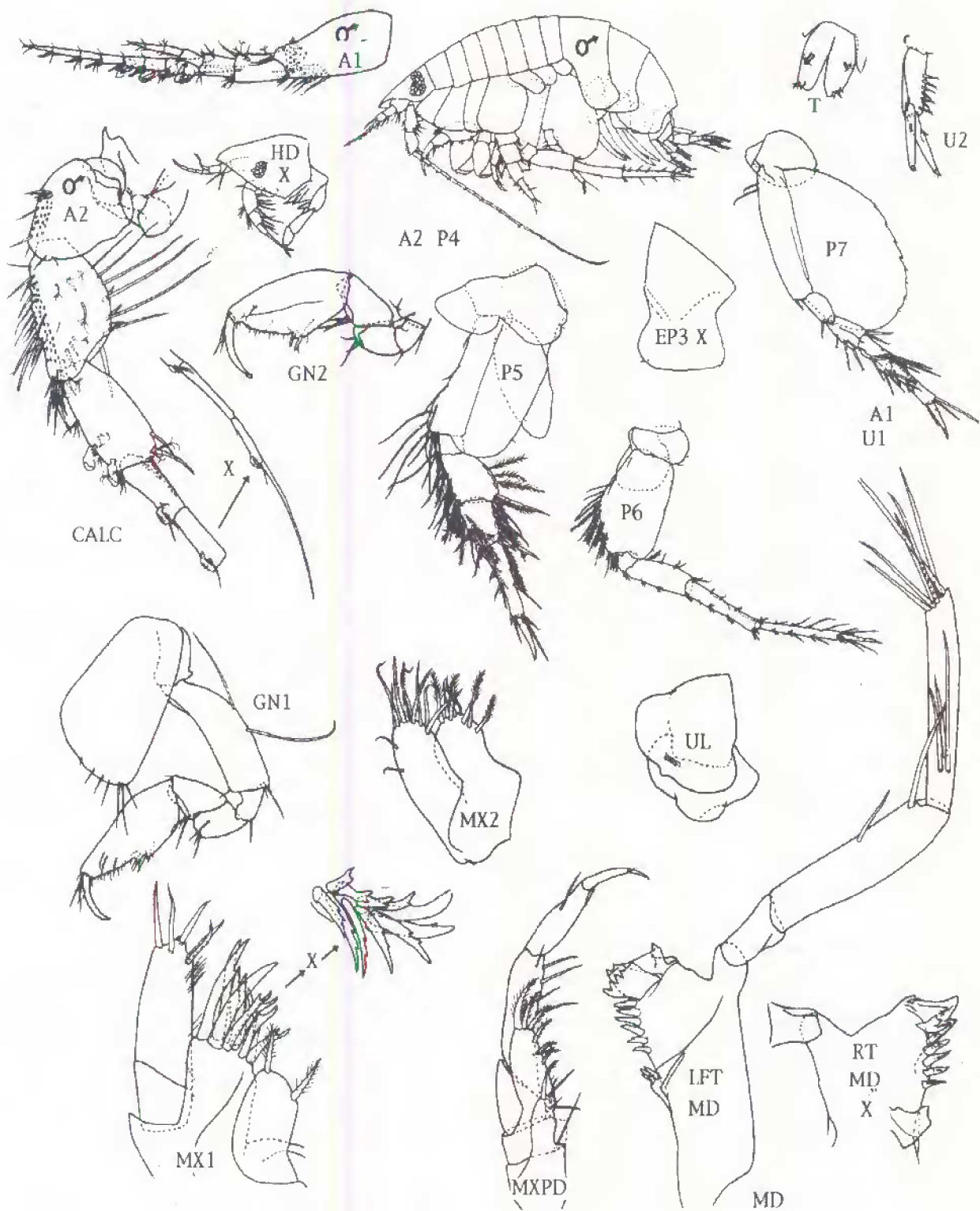


FIG. 17. *Paraphoxus* species 2. Male (3.3 mm); Female (3.3 mm). Hong Kong. (modified from Hirayama, 1992)

Mandibular molar with 3 apical spines; spine row with 8 thick blades; mandibular palp segment 3 with 1-2 baso-facial "A" setae. Maxilla 1, outer plate with 11 apical spines; palp 2-segmented. Maxilliped outer plate very narrow, 2 apical spines large.

Coxa 1 distally splayed, lower margin with 10+ setae. Gnathopod propods subsimilar. Gnathopod 1, basis with 8-10 long hind marginal setae. Gnathopod 2, hind lobe of carpus free, with 2 marginal setae.

Peraeopods 3 & 4, postero-distal pair of spines of segment 5 strong, longer than segment 6, inner margin with 3 spines; dactyl medium, slightly shorter than segment 6. Peraeopod 5, basis medium broad, hind margin nearly straight; segment 6, anterior margin with 2 spines, posterior margin unarmed. Peraeopod 6, segments 5 & 6 not elongate, margins collectively with about 8 clusters of spines and long setae. Peraeopod 7, basis medium broad, hind margin with 6-7 weak teeth.

Pleon plate 3 somewhat produced, but very broadly rounded behind, devoid of marginal setae. Uropods 1 & 2, rami with 1-2 marginal spines. Uropod 1, peduncle with 2-3 baso-facial setae. Uropod 2, peduncle with 2 outer marginal spines. Uropod 3, peduncle with few (2-3) distal fan spines; inner ramus about 1/2 length of outer ramus; terminal segment medium-long, with single long apical seta.

Telson lobes slender, each with 2 slender apical spines.

Male penult. (3.5 mm). In one specimen, the outer plate of maxilla 1 had 10 apical spines. Adult male not present in material at hand.

Etymology: The species name alludes to its relative frequency at the type locality on Vancouver I., Pacific coast of British Columbia.

Distribution: Known only from southern Vancouver I. (Berkeley Sound and Victoria Roads) at depths of 15-45 m.

Taxonomic Commentary: This species is clearly a member of the *oculatus* group, but is distinguished from the type species by the molar spines, form of pleon plate 3, and weak lower marginal setation of coxa 1. Several variants were noted in size (3.2- 3.6 mm) and in some character states of material from Berkeley Sound, and in 1 lot from southeastern Alaska. In these, the number of marginal setae of coxa 1 was generally greater (7-9), and the posterior lobe of pleon plate 3 more pronounced, but otherwise little different from the type material. The material of Staude (loc. cit) and records of Austin (1985) may be referable in part to this species.

Paraphoxus tomiokaensis Hirayama
(Fig. 19)

Paraphoxus tomiokaensis Hirayama, 1987: 42, figs. 254-256.

Diagnosis. The figures of Hirayama (loc. cit.) are detailed and accurate, and are utilized here to supplement the original description with character states of the keys and numerical taxonomical analysis (p. 105).

Female (4.0 mm): Rostrum short, apex subacute, reaching little beyond peduncle 1 of antenna 1. Antenna 1, flagellum 7-8 segmented, accessory flagellum 4-segmented. Antenna 2, segment 4 with distal facial fan of 8 spines, flagellum 6-7 (?) segmented.

Mandibular molar with 4 thick apical spines; spine row of 7 short thick blades; palp segment 3 with 3-4 baso-facial "A" setae. Maxilla 1, outer plate with 11 apical spines; palp 1-segmented (?). Maxilliped, outer plate tall, distal 3 spines large.

Coxal plate 1, with 8 distal marginal setae. Coxa 4 deeper than broad, hind margin convex. Gnathopods subsimilar in size and form. Gnathopod 1, basis with 2-3 long posterior marginal setae only.

Peraeopods 3 & 4, penultimate postero-distal spine strong, length slightly less than segment 6; dactyl stout, length about 80% of segment 6, having 2 inner distal spine groups. Peraeopod 5, basis medium broad, hind margin straight; segment 6 with 2 strong anterior marginal spine clusters.

Peraeopod 6, segments 5 & 6 not shortened, margins collectively with about 10 clusters of spines and setae. Peraeopod 7, basis postero-distally extended, hind margin with 6-7 weak teeth.

Pleon plate 3, hind corner not produced, broadly rounded, convex below. Uropods 1 & 2, rami weakly armed, rami with 1-2 marginal spines. Uropod 1, peduncle with 4 baso-facial setae. Uropod 3, peduncle with distal fan of 3-4 medium spines; inner ramus short, broad, terminal segment of outer ramus short.

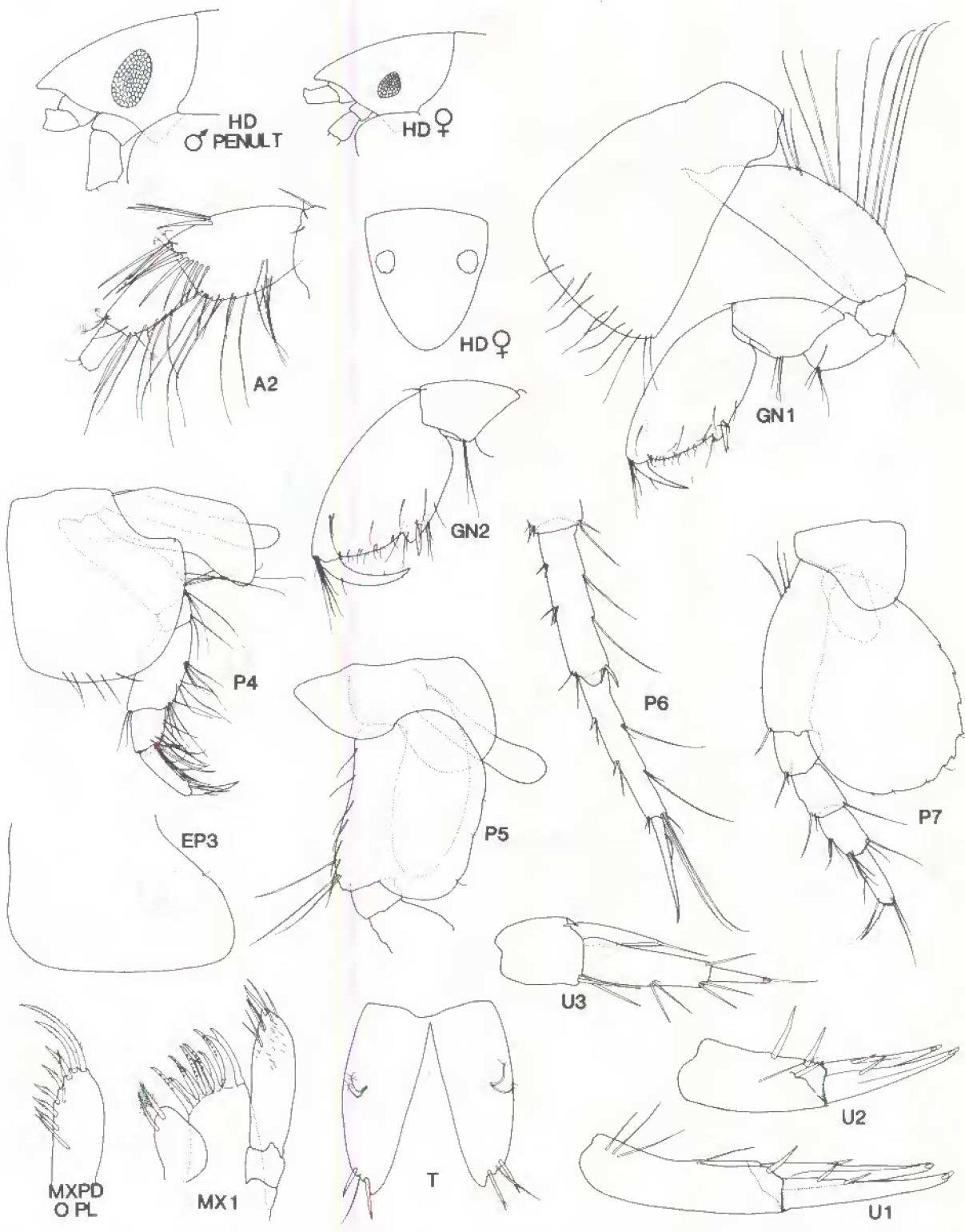
Telson lobes not broadened, each with 2 apical spines.

Distribution: Ariake Sea, Japan.

Taxonomic Remarks: *P. tomiokaensis* evinces more plesiomorphic character states than any other member of the *oculatus* subgroup (p. 99). It appears to be most closely related to *Paraphoxus* species 2, recorded and described as *P. oculatus* from Hong Kong by Hirayama (1992). *P. tomiokaensis* differs from the type species, *P. oculatus*, in characters of the key (p. 98), and in the very different form of pleon plate 3, and basis of peraeopod 5.

FIG. 18. *Paraphoxus communis*, new species.
FEMALE ov (3.4 mm) HOLOTYPE; MALE (3.5 mm)
Berkeley Sound, B. C. (SEE PAGE 105-OPPOSITE)

FIG. 19. *Paraphoxus tomakiensis* Hirayama, 1987.
FEMALE (4.0 mm); MALE (3.75 mm). JAPAN.
(SEE PAGE 106)



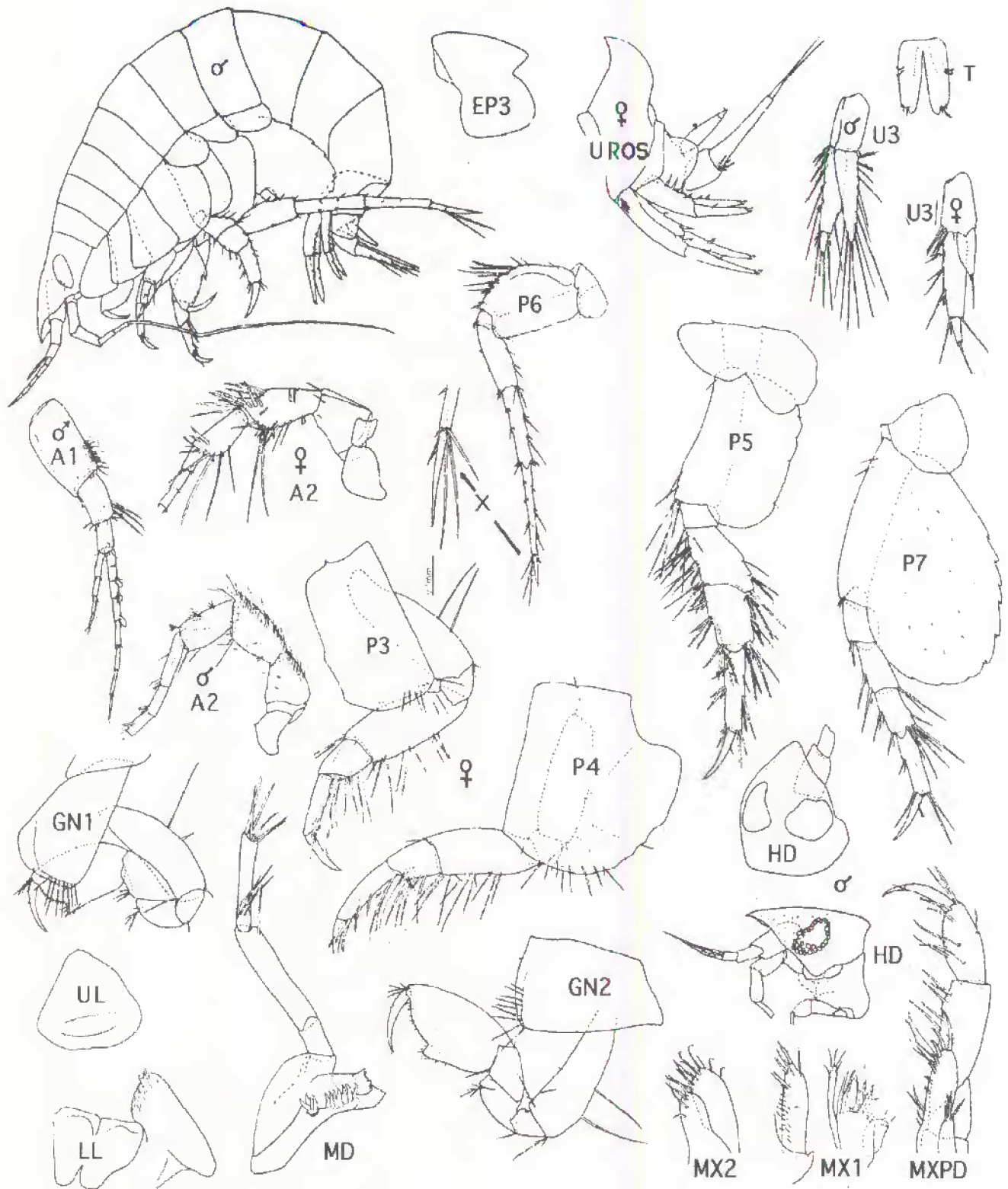


FIG.19. *Paraphoxus tomiokaensis* Hirayama. Male (3.5 mm). Female (4.0 mm). Japan. (after Hirayama, 1987)

Paraphoxus gracilis, new species
(Fig. 20)

Material Examined:

BRITISH COLUMBIA: Southeastern Mainland coast: Queen Charlotte Channel, off Passage Island, ELB Sta. P8, 130 m., Nov. 3, 1977. - 1 mature male; Sta. P7, 250 m. - 1 mature male; Strait of Georgia, off Passage I., 160 m - 1 female (ov.). Mouth of Burrard Inlet, ELB Stn. P4, 225 m, Nov. 2, 1977 - 1 female ov. (3.0 mm) with slide mount (fig'd), HOLOTYPE. CMN Cat. No. NMCC1992-1126; 1 mature male (3.75 mm), with slide mount (fig'd) ALLOTYPE. CMN Cat. No. NMCC1992-1127. Indian Arm, ELB Stn. E5, 60 m., Nov. 4, 1977 - 1 male, mature.

Diagnosis Female ov. (3.0 mm): Rostrum medium, apex subacute, reaching nearly to peduncular segment 3 of antenna 1. Eye very small, round. Antenna 1, flagellum with 6-7 segments, accessory flagellum with 4 segments. Antenna 2, peduncular segment 4 with distal facial fan of 9-10 fossorial spines; flagellum 6-segmented.

Mandibular molar with 3 apical spines; spine row with 6-8 blades; palp segment 3 with 1-2(?) baso-facial "A" setae. Maxilla 1, outer plate with 11 apical spines; palp distinctly 2-segmented, apex appearing subacute. Maxilliped, outer plate, apex with 2 long pectinate spines.

Coxa 1 with 8-9 distal marginal setae. Coxa 4 broad, hind margin steeply and strongly convex. Gnathopod 1, propod smaller and more slender than in gnathopod 2; basis with 8-10 long posterior marginal setae. Gnathopod 2, carpus short, hind margin not cryptic, with 3-4 posterior setae.

Peraeopods 3 & 4, segment 6, postero-distal pair of spines slender, subequal, length about equal to segment 6; dactyls medium, length about 80% segment 6. Peraeopod 5, basis broad, hind margin nearly straight; segment 6 with 1-2 anterior marginal spines and 2 posterior marginal setae. Peraeopod 6 slender, segments 5 & 6 well armed, margins collectively with about 12 clusters of short spines and longish setae. Peraeopod 7, basis medium broad, hind lobe not deep, hind margin with 7-8 small teeth.

Pleon plate 3, hind corner produced, rounded, lower margin straight, hind margin with a few short setae. Uropods 1 & 2, rami with 1-2 slender spines. Uropod 1, peduncle with 3 baso-facial setae. Uropod 2, peduncle outer margin with 3 long spines. Uropod 3, peduncle with distal fan of 5 long spines; outer ramus about twice length of inner ramus; terminal segment slender, about half length of proximal segment, apex with 1 long and 1 short seta.

Telson lobes relatively broad, acute, each apically with 2 long slender spines.

Male (3.75 mm). Eyes large, vertically subovate. Antenna 1, proximal 3-4 flagellar segments calceolate. Antenna 2, peduncular segment 4 with weak antero-distal fan of spines; peduncular segment 5 with 2 antero-distal calceoli; flagellum medium, 18-segmented, proximal 3, and alternate

distal segments calceolate. Peraeopod 7, segment 5 with 2 slender postero-distal copulatory spines; segment 6, distal margin gently convex, minutely pectinate.

Etymology: From the Latin *gracilis*, alluding to the relatively slender spines and appendages of this species.

Distribution: Known only from the environs of Burrard Inlet and Howe Sound, in deep muddy bottoms (60 - 160 m).

Taxonomic Commentary: Basically a member of the *oculatus* group but with character states (e.g. of gnathopods, and broadened telson lobes) transitional to the more advanced *pacificus* group. In mature males, the flagellum of antenna 2 (male) is relatively short (< 20 segments).

Paraphoxus pacificus, new species
(Fig. 21)

Material Examined. A total of 11 females and 6 subadult males, as follows:

S. E. ALASKA: ELB Sta. A103, Unakivit Inlet, near mouth of Siwash bay, 20-40 m, mud and stones, July 5, 1961 - female (3.75 mm), male (3.0 mm), slide mounts, 2 subadult males (3.0 mm), 2 females, 2 male subadults.

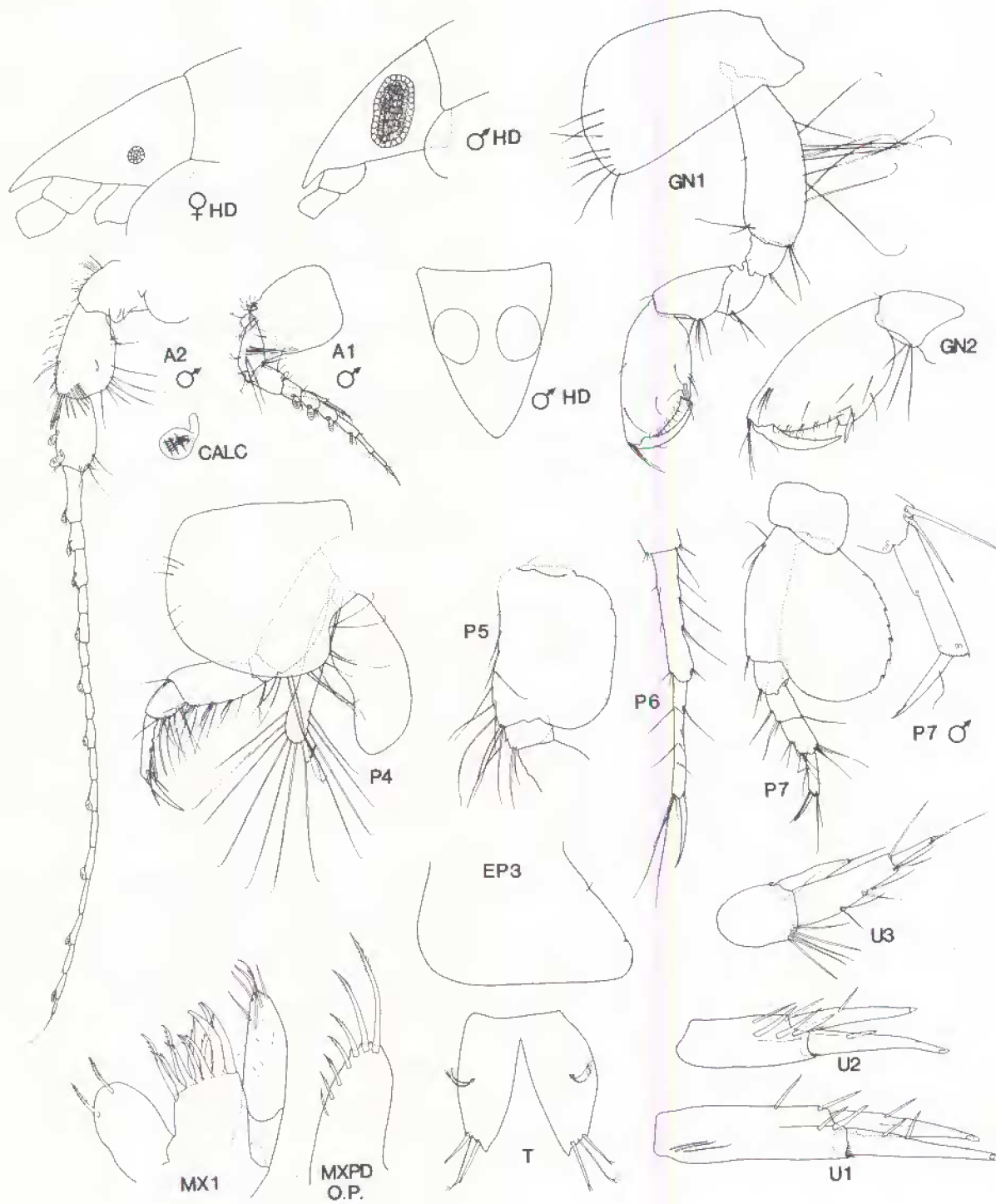
BRITISH COLUMBIA: Vancouver Island: Berkley Sound, North of Diana Island, ELB Stn. B26, 25-25 m., July 8, 1976 - 1 female, interbrood (3.6 mm), with slide mount (fig'd), HOLOTYPE, CMN Cat. No. NMCC1992-1119; 1 male subadult (3.0 mm) with slide mount (fig'd) ALLOTYPE, CMN Cat. No. NMCC1992-1120; 1 female ov. (4.0 mm) with slide mount (mouth parts fig'd), + 6 other females and 1 subadult male, PARATYPES, CMN Cat. No. NMCC1992-1121. Edward King I., ELB Stn. B28, LW level, *Phyllospadix* zone, July 10, 1976 - 1 male subadult (3.75 mm).

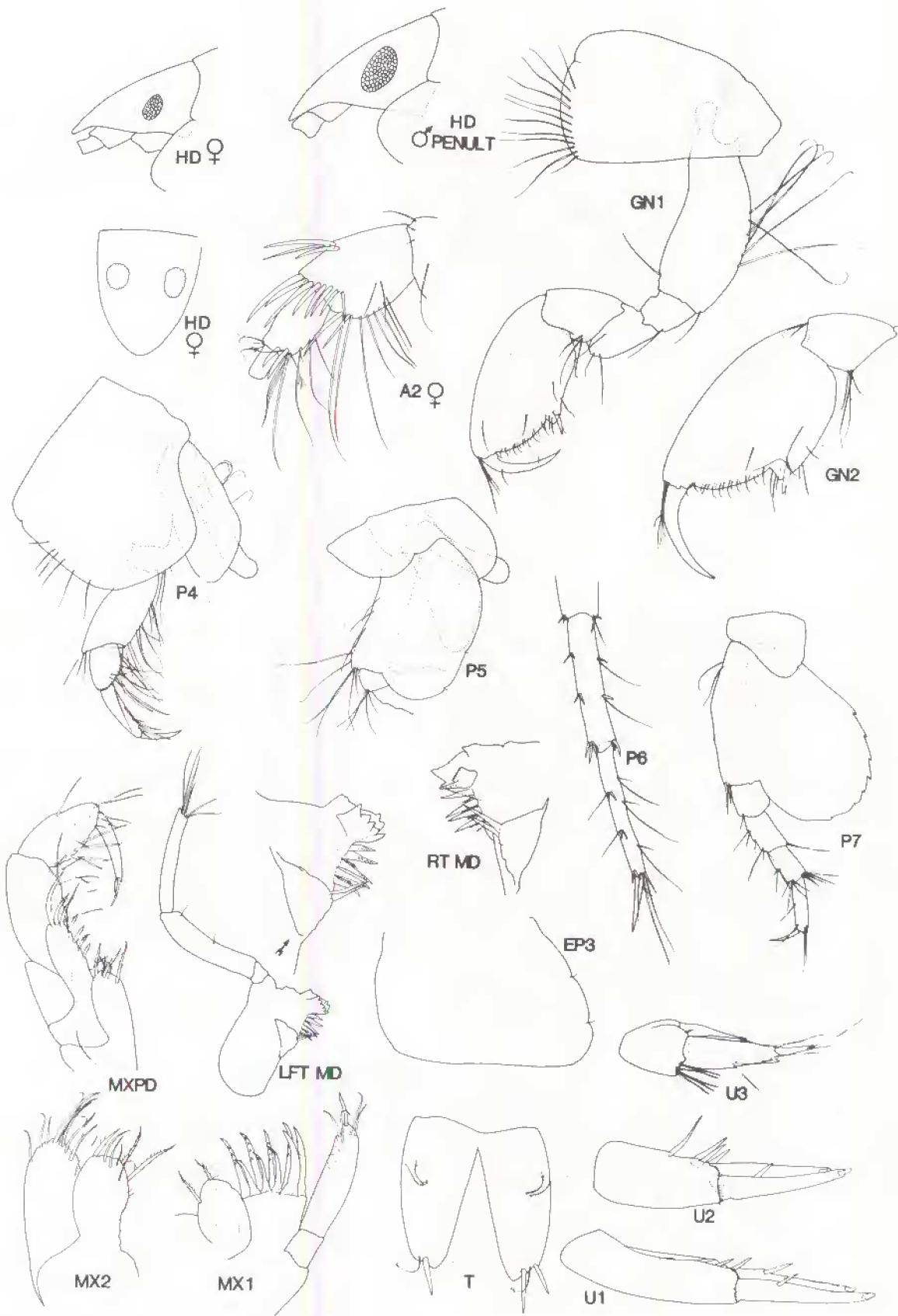
Diagnosis Female (3.6 mm): Rostrum medium long, bluntly rounded apex reaching peduncular segment 3 of antenna 1. Eyes relatively large, oval, about 40-faceted. Antenna 1, flagellum 6-segmented; accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 with distal facial cluster of about 8 fossorial spines; flagellum 6 segmented.

Mandibular molar with 2-3 elongate spines; spine row with 5 stout blades; palp segment 3 with 1-2 baso-facial setae. Maxilla 1, outer plate with 9 apical spines; palp 2-segmented.

FIG. 20. *Paraphoxus gracilis*, new species.
FEMALE ov (3.0 mm) HOLOTYPE; MALE (3.7 mm)
ALLOTYPE. (SEE PAGE 108).

FIG. 21. *Paraphoxus pacificus*, new species.
FEMALE ov (3.6 mm) HOLOTYPE; MALE (3.0 mm)
(SEE PAGE 109).





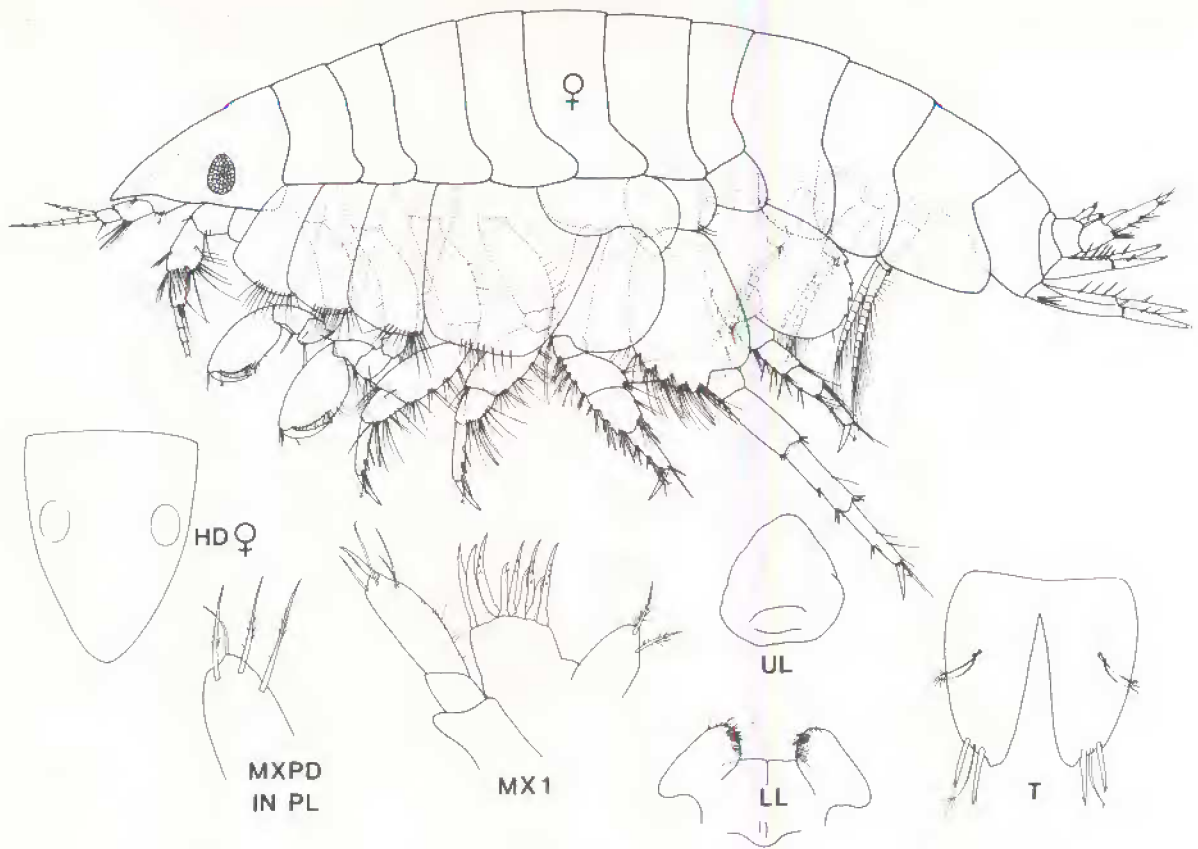


FIG. 22. *Paraphoxus similis*, new species. Female (3.5 mm). Berkeley Sound.

Coxa 1, with 8-12 distal marginal setae. Coxa 4 broad, hind margin obtuse. Gnathopod propods strongly dissimilar in size and form. Gnathopod 1, propod shorter and more slender than in gnathopod 2; carpus relatively short, with 3 hind marginal setae; basis with about 6 long posterior marginal setae. Gnathopod 2, carpus with 3 posterior marginal setae.

Peracopods 3 & 4, postero-distal spines of segment 5 strong, subequal in length to segment 6; dactyl short, about 2/3 length of segment 6. Peracopod 5, basis broad, hind margin convex, with very shallow median indentation; segment 6 with 2 anterior marginal spines and 0-1 posterior marginal setae. Peracopod 6, distal segment slender, segments 5 & 6 collectively with 9 marginal clusters of single spines and long seta. Peracopod 7, basis medium, with about 8 weak hind marginal teeth.

Pleon plate 3 not strongly produced behind, hind margin steeply oblique, with 2 small setae, lower margin almost straight. Uropods 1 & 2 weakly armed, rami with 0-1 marginal spines. Uropod 1, peduncle with 1-2 baso-facial setae. Uropod 2, peduncular outer margin with 3 stout spines. Uropod 3, peduncle with distal fan of 5-6 slender spines; outer ramus broad, less than twice length of inner ramus; terminal segment medium, with 1 short and 1 long apical setae.

Telson lobes narrowing distally, each with 1-2 slender apical spines.

Male, penult. (3.0 mm): No special features noted.

Etymology: The name alludes to the species endemicity in the North Pacific region.

Taxonomic-Distributional Commentary: This advanced species ranges from the north side of Prince William Sound, S.E. Alaska, to southern British Columbia, at outer coast localities. This species and *P. simplex* characterize the advanced Pacific-endemic species complex in having gnathopod propods dissimilar, dactyls of peracopods 3 & 4 short, blades of the mandibular spine row few and stout, and the outer plate of maxilla 1 with 9 apical spines.

Paraphoxus similis, new species
(Fig. 22)

Material Examined:

BRITISH COLUMBIA: Berkeley Sound, off Diana island, ELB Stn B26, Depth 24-35 m, shelly mud and stones, July 8, 1976 - 1 female ov. (3.5 mm), with slide mount (fig'd), HOLOTYPE, CMN Cat. No. NMCC1992-1118.

Diagnosis. Female (3.5 mm): Rostrum long, subacute, apex reaching to peduncular segment 3 of antenna 1. Eye medium, almond-shaped. Antenna 1, flagellum 6-segmented; accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 with distal fan of 7-8 fossorial spines; flagellum of 6(?) segments.

Mandibular molar with 3(?) apical spines; spine row with 8(?) blades; palp segment 3 lacking (?) basofacial setae. Maxilla 1, outer plate with 9 apical spines; palp 2-segmented. Maxilliped, inner plate with 3 apical plumose setae.

Coxa 1, distal margin with 10-12 setae. Coxa 4 broad, hind margin oblique, nearly straight. Gnathopod propods dissimilar in size and form, that of gnathopod 1 smaller and more slender; carpus with free posterior border.

Peraeopods 3 & 4, penultimate postero-distal spine of segment 5 strong, slightly shorter than segment 6; dactyl slender, about 3/4 length of segment 6. Peraeopod 5, basis very broad, hind margin strongly convex; segment 6, anterior margin with 2 spines, hind margin bare. Peraeopod 6, distal segments not elongate, segments 5 & 6 nearly bare, margins collectively with only 5-6 clusters of spines and setae. Peraeopod 7, basis broad behind, margin with 6-8 weak teeth.

Pleon plate 3, hind corner produced, broadly rounded, lower margin straight. Uropods 1 & 2, rami shorter than peduncles, with 1-2 marginal spines. Uropod 1, peduncle with 3 slender baso-facial setae. Uropod 2, peduncular outer margin with 4-5 stout spines. Uropod 3, peduncle with distal fan of 3-4 medium spines; inner ramus about half the length of the outer ramus, terminal segment small (1/3 proximal segment).

Telson little longer than wide, lobes broad basally, apex with 2 medium stout spines (and seta).

Etymology: From the Latin "*similis*" - like, alluding to its overall similarity to the morphologically more advanced species of *Paraphoxus*.

Taxonomic-Distributional Commentary. This species, known only from a single specimen from Berkeley Sound, B. C., is basically a member of the *pacificus* subgroup of *Paraphoxus*. Its character states are mainly apomorphic and thus only remotely related to the type species *P. oculatus*.

Paraphoxus rugosus, new species
(Fig. 23)

Material Examined:

ALASKA: Beaufort Sea (off the mouth of the McKenzie River, Yukon Territories), Aug. 24-28, 1986, M. Gordon, ERA coll., 147-275 m. bottom dredge: A total of 17 females, 5 males, and 34 juveniles, at 10 stations, as follows: BDS86-D1-002, 226 m. - 1 penult male, 1 im; *Ibid*-003, 152 m. - 1 female ov. (4.75 mm), with slide mount (fig'd) HOLOTYPE, CMN Cat. No. NMCC1992-1128; 1 female, 20 juveniles; *Ibid*-017, 240 m. - 1 male penult.; *Ibid*-021, 275 m. - 1 male subadult; *Ibid*-028, 231 m. - 1 female with slide mount, 7 females, 8 juvs. *Ibid*-030, 222 m. - 1 female ov., 1 im. BDS86-D2-006, 157 m. - 1 female (br. II), 2 im.; *Ibid*-018, 147 m. - 1 female; *Ibid*-024, 155 m. - 2 females; *Ibid*-028, 231 m. - 1 male penult (4.4 mm) with slide mount

(fig'd), ALLOTYPE, CMN Cat. No. NMCC1992-1130; 1 male penult. (3.9 mm), PARATYPE, CMN Cat. No. NMCC1992-1131; 1 female Br. II., 1 male im.

Diagnosis (Female, 4.75 mm): Rostrum relatively long, subacute apex reaching to peduncular segment 3 of antenna 1. Eye relatively large, vertically subovate. Antenna 1, flagellum 7-segmented; accessory flagellum 4-segmented. Antenna 2, peduncle 4 with distal facial fan of 7-8 stout fossorial spines; flagellum 6-segmented.

Mandibular molar with 3 apical spines; spine row with 6 stout blades; palp segment 3 with 1-2 baso-facial setae. Maxilla 1, outer plate with 9 apical spines; palp 2-segmented, apex subconical. Maxilliped, outer plate strong, distally with 4 large pectinate spines.

Coxa 1, with 11-12 distal marginal setae. Coxa 4 deep, short, convex hind margin steeply sloped. Gnathopod propods strongly dissimilar in size, less so in form. Gnathopod 1, basis with 3 long posterior marginal setae. Gnathopod 2, carpus, hind margin cryptic, with 2 long setae.

Peraeopods 3 & 4, postero-distal spines of segment 5 long and heavy, exceeding length of segment 6; dactyls short, about 2/3 length of segment 6. Peraeopod 5, basis very broad, hind margin gently convex; segment 6 anterior margin with 2 spines, hind margin with 0-1 setae. Peraeopod 6, distal segments relatively short, well armed, segments 5 & 6 collectively with 12-13 clusters of spines and long setae. Peraeopod 7, basis produced postero-distally, hind margin with about 12 weak teeth.

Pleon plate 3 little produced behind, broadly rounded, hind margin with 3 small setae, lower margin gently convex. Uropods 1 & 2, rami with 1-2 marginal stout spines. Uropod 1, peduncle with 4 slender baso-facial setae. Uropod 2, outer margin with 4 spines. Uropod 3, peduncle with distal fan of 7-8 long spines; outer ramus large (2X inner), terminal segment short, with 1 long and 1 medium apical setae.

Telson lobes relatively broad, each with pair of medium slender spines.

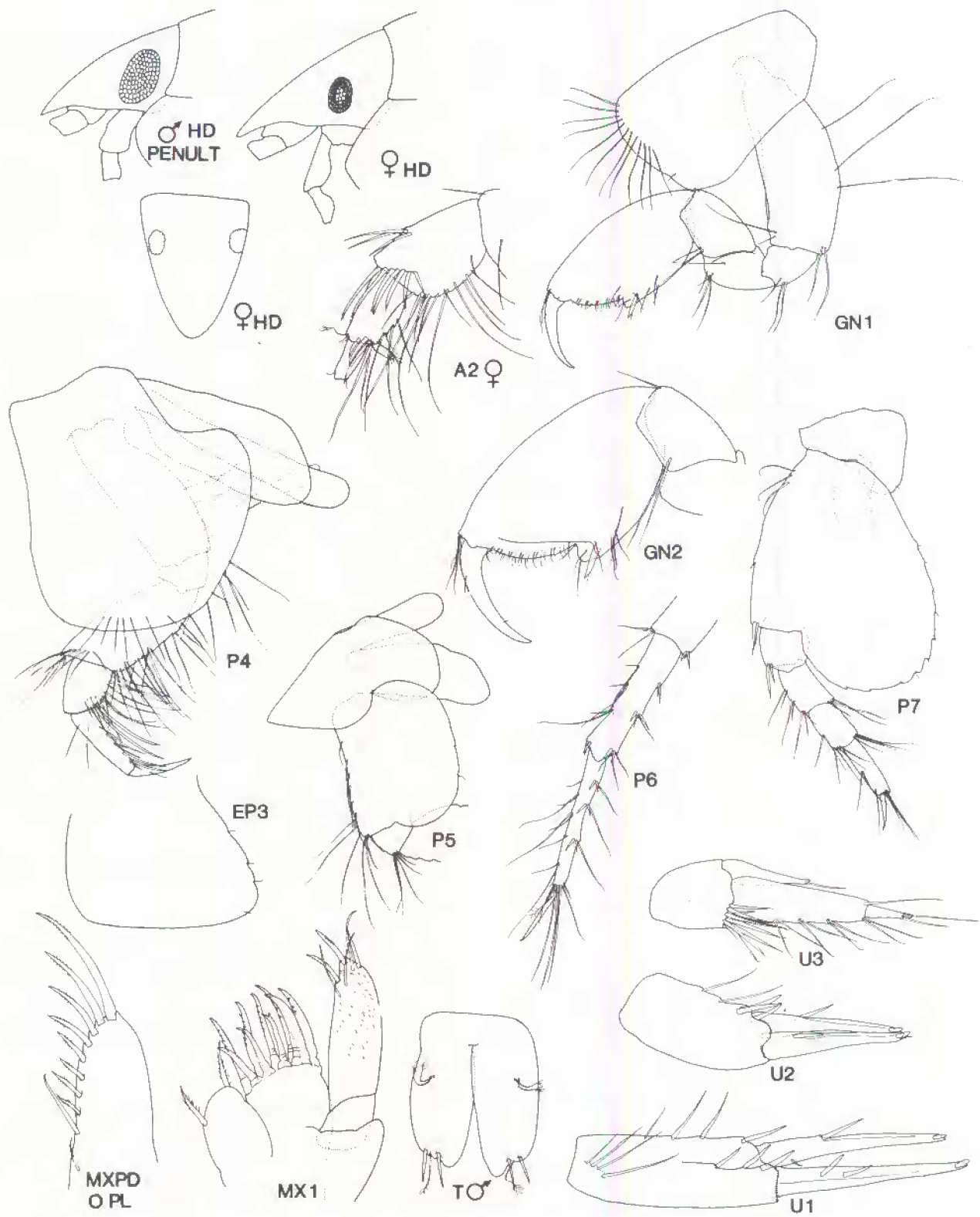
Male, penult. (4.4 mm): No taxonomically special features were noted.

Etymology: From the Latin *rugosus* meaning "rugged", referring to the heavy armature of antennae and peraeopods.

Distribution: Known only from the above locations in the southeastern part of the Bering Sea, in fine sandy muds, to depths of 275 m.

Taxonomic commentary: The species is basically a member of the advanced *pacificus* group but entrains some morphological plesiomorphies that include the rich armature of appendages, and relatively large eyes.

FIG. 23. *Paraphoxus rugosus*, new species.
FEMALE ov (3.6 mm) HOLOTYPE; MALE (3.0 mm)
(SEE PAGE 112)



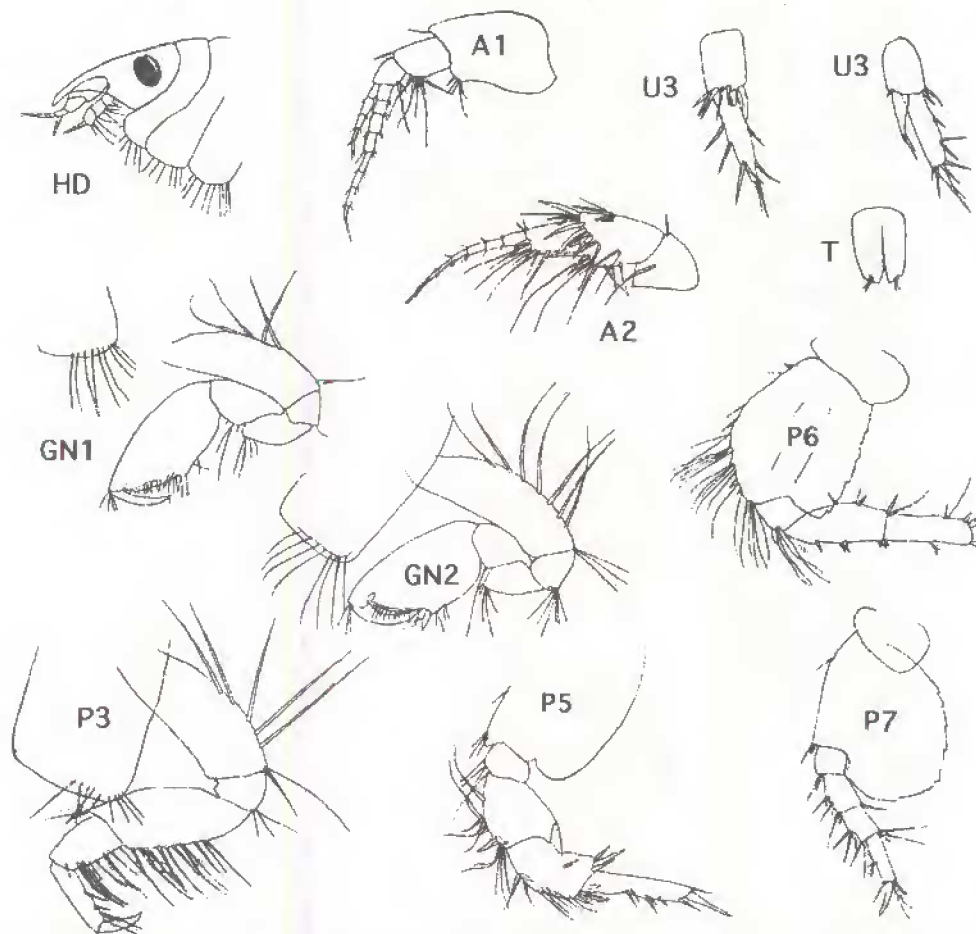


FIG. 24. *Pararhinus simplex* Gurjanova. Female ov. (6.0 mm). Japan Sea.

Pararhinus simplex (Gurjanova)
(Fig. 24)

Pararhinus simplex Gurjanova, 1938: 272, fig. 10.—
Gurjanova, 1951: 392, fig. 238.

Pararhinus simplex Barnard & Karaman, 1991: 625.

Diagnosis: Since this species was not identified in present study material, the diagnosis is adapted from the description and figures of Gurjanova (*loc. cit.*).

Female (6.0 mm): Rostrum long, tip reaching end of peduncle of antenna 1. Eye medium, vertically oval. Antenna 1, flagellum 8-9 segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 short, with distal facial cluster of 8-9 stout fossorial spines; flagellum 8-9 segmented.

Mouthparts not described or figured but are here presumed to be similar to those of *P. beringiensis* (p. 114) (i.e., mandible with 3 molar spines, about 5 blade spines; maxilla 1, outer plate with 9 apical spines, palp 2-segmented).

Coxa 1 with 9 distal marginal setae. Gnathopod propods somewhat dissimilar in size and form, that of gnathopod 1 long and more slender, that of gnathopod 2 shorter and deeper; carpus of gnathopod 1 with 2-4 hind marginal setae, carpus of gnathopod 2 with 1-2 long setae; basis of gnathopod 1 with 4 long posterior marginal setae.

Peraeopods 3 & 4, postero-distal spines of segment 5 subequal, slender, length about equal to segment 6 dactyl short, length about 60% of segment 6. Peraeopod 5, basis medium broad, hind margin convex; segment 6, anterior margin with 3 spine groups, hind margin bare. Peraeopod 6, distal segments short, relatively stout, margins sparsely setose-spinose collectively probably with only 5-6 marginal spine and setal clusters. Peraeopod 7, basis little broadened behind, with about 10 weak marginal teeth.

Pleon plate 3 and uropods 1 & 2 not shown. Uropod 3, peduncle with distal fan of 5 stout spines; inner ramus very short, length < 1/2 outer ramus; terminal segment medium, apex with 1 long and 1 medium slender seta.

Telson lobes medium broad, with single apical spine.

Male: unknown.

Distribution: Known only from the Russian coast of the, Sea of Japan, in the *Phyllospadix* zone.

Taxonomic Commentary: The advanced species is closely similar to *P. beringiensis* (below) but differs in several respects (see key). The eye is much larger, the armature of the peduncle of antenna 2 is slightly less strong, and the lower margins of the coxal plates are distinctly more heavily setose.

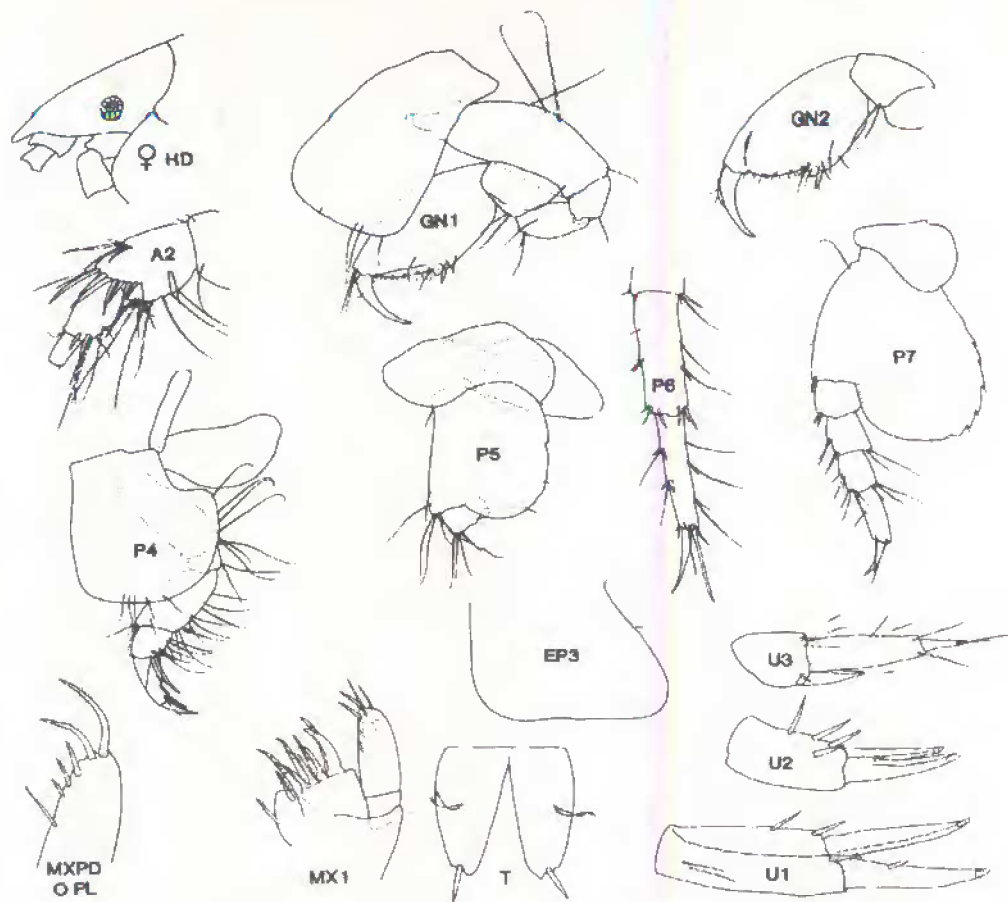


FIG. 25. *Paraphoxus beringiensis*, new species. Female br. II (2.75 mm). Bering Sea.

Paraphoxus beringiensis, new species
(Fig. 25)

Material Examined:

ALASKA: Bering Sea off St. Lawrence I., 45 m. sand, July 1, 1980 - 1 female br. II (2.75 mm), with slide mount HOLOTYPE (fig. 'd), 1 other female. CMN Cat No. NMCC1992-1122.

Diagnosis: Female br. II (2.75 mm): Rostrum short, apex reaching little beyond peduncular segment 1 of antenna 1. Eye small, round. Antenna 1, flagellum 5-segmented; accessory flagellum 4-segmented. Antenna 2, peduncle 4 with distal cluster of 8-9 strong facial fossorial spines; flagellum 5-segmented.

Mandibular molar with 3 apical spines; spine row with 4-6 stout blades; palp segment 3 with 2-3 baso-facial setae. Maxilla 1, outer plate with 9 apical spines, palp 2-segmented, short, weakly armed apically. Maxilliped, outer plate, distal 2 apical spines strong, sharply curved.

Coxa 1 with 4-5 distal marginal setae. Coxa 4 short, deep, hind margin steeply convex. Gnathopod propods subsimilar in size, that of I more slender, but not shorter than 2. Gnathopod 1, carpus short, with 2 posterior marginal setae; basis with 3 long hind marginal setae.

Peraeopods 3 & 4, penultimate postero-distal spine of segment 5 stout, length nearly equal to segment 6; dactyls

short, about 2/3 length of segment 6. Peraeopod 5, basis very broad, hind margin distinctly convex, weakly notched; segment 6, anterior margin with cluster of 3 strong spines, hind margin bare. Peraeopod 6, distal segments short, relatively stout, segments 5 & 6 collectively with about 9 clusters of short spines and/or long setae. Peraeopod 7, basis expanded posteriorly, with about 10 very weak hind marginal teeth.

Pleon plate 3, hind corner somewhat produced, rounded, lower margin straight. Uropods 1 & 2, rami nearly unarmed, each with 0-1 marginal spines. Uropod 1, peduncle with 2 slender baso-facial setae. Uropod 2, peduncular outer margin with 3 stout spines. Uropod 3, peduncle with weak distal fan of 3-4 slender spines; inner ramus very short, less than half outer ramus; terminal segment medium, apex with 1 long and 1 medium slender seta.

Telson lobes broad, each with 1 stout apical spine.

Etymology: The name alludes to the Bering Sea where the species may be endemic.

Taxonomic and Distributional Commentary: The species has been taken only at St. Lawrence I. in the Bering Sea. It is closely similar to *P. simplex* Gurjanova from the Sea of Japan (p. 113) but differs in characters of the key (p. 98), and in the plesiomorphically subsimilar gnathopod propods.

PHOXOCEPHALINAE Barnard & Drummond

Phoxocephalidae Sars, 1895: 142 (partim).—Gurjanova, 1951: 361 (partim).

Phoxocephalinae: Barnard & Drummond, 1978: 416.—Barnard & Karaman, 1991: 592 (key to genera).

Type genus. *Phoxocephalus* Stebbing, 1888: 810.

Genera. (North Pacific region): *Cephalophoxoides* Gurjanova, 1977 [81]; *Metaphoxus* Bonnier, 1896 [630]; *Parametaphoxus* Gurjanova, 1977 [81].

Diagnosis: Rostrum well developed, hood-like, lacking lateral incisions. Pigmented eyes usually present in male, often small or lacking in female. Antenna 1, segment 2 shortened, but longer than segment 3; segments of accessory flagellum and flagellum transversely separated; in male, peduncular segment 1 with strong posteromedial cluster of brush setae ("fuzz" of Barnard & Drummond); basal segments of flagellum calceolate and/or callynophorate. Antenna 2, peduncular segments 4 & 5 short to medium, 4 with distal facial fan of stout spines, posterior margin slender-spinose; in male, segments 3 & 4 with anterior marginal brush setae, segment 5 with anterior submarginal calceoli; flagellum usually elongate and calceolate, distally on alternate segments.

Mandibular molar mostly non-tritulative, bearing 4 or fewer tightly clumped apical spines; left lacinia 5-6 dentate; right lacinia various; blades strong, numerous; palp slender, segment 3 with few or no "A"-seta. Maxilla 1, outer plate with 7-11 apical spines, inner plate with 0-2 apical setae. Maxilla 2, inner plate small. Maxilliped, inner and outer plates reduced, outer with stout inner marginal raptorial spines; palp ordinary, inner margins lacking stout spines; dactyl slender, curved, nail elongate.

Coxae 1-4 broad, deep, lower margin setose. Gnathopods medium, strongly subchelate, subequal; carpus short-eusiroid, propod palm oblique, smoothly convex; in gnathopod 1, propod usually more slender and carpus slightly longer than in gnathopod 2.

Peraeopods 3 & 4, segments 4 & 5 stout, segment 5 short, postero-distal setae increasingly strong, usually spine-like; segment 6 slender (not spatulate) weakly armed, dactyls elongate. Peraeopod 5, basis variously expanded (narrow in harpiniid subgroup); segments 4 & 5 variously expanded and facially spinose. Peraeopod 6 elongate, basis broadest medially; segments 4, 5, & 6 slender or little expanded, usually elongate. Peraeopod 7 short, basis broadly expanded posteriorly but not deeply, lower margin exceeded fully by segments 5-7; segment 5 (male), anterior margin may be incised and/or bearing stout copulatory spines.

Pleon plate 3, hind corner variously subquadrate, rounded, or produced, outer facial and lower margin lacking rows of long setae. Pleopod peduncles slightly broadened, margins smooth. Uropods 1 & 2 and pleopods normal, peduncles

little broadened, margins bare. Uropods 1 & 2 medium, peduncle and rami subequal in length; peduncle with basofacial spine cluster, weak disto-lateral spine (not enlarged or spike-like), and distal comb-like lobes; rami subequal (inner shorter), unmodified, with 0-3 marginal spines and single short apical spine semi-fused with ramus. Uropod 3 parviramous (female) rami slender, outer much the longer, terminal segment large; in male, rami acquiramous subequal, margins plumose-setose.

Telson lobes narrow, separated to base, apices usually with 1-3 short spines and 1-3 supernumerary setae. Coxal gills medium to large on peraeopods 2-5, smaller on peraeopods 6 & 7. Brood plates, small, narrow, not broadened distally.

Taxonomic Remarks: Barnard & Karaman (1991) have provided an up-dated list of about 20 generic inclusions within subfamily Phoxocephalinae (world-wide). These genera encompass mostly Australian taxa, described initially by Barnard & Drummond (1978, loc. cit.) and taxa from other regions of the southern hemisphere including Madagascar. Records of the genera *Leptophoxus*, *Hopiphoxus*, and *Coxophoxus* from deep waters off southern California and Baja California are few and isolated. The latter genus was transferred to its own family, Coxophoxidae, by Gurjanova (1977). In this study, it is given intermediate taxonomic recognition, as subfamily Coxophoxinae.

Genera presently assigned to subfamily Phoxocephalinae exhibit a wide variety of mouthpart character states (see Barnard & Drummond, 1978). Thus, molars are fully tritulative in a number of genera, including *Phoxocephalus* (the type), but are small and non-tritulative in others (e.g. *Limnoporeia*). In most genera, however, the mandibular blades are short and thick. The present subfamily concept must eventually meet the rigorous test of conformity within other major character states, particularly of the male copulatory apparatus, as these phyletically significant taxonomic features become better known.

Phoxocephalus Stebbing

Phoxocephalus Stebbing, 1888: 810.—Gurjanova, 1977: 82.—Barnard & Drummond, 1978: 417.—Barnard & Karaman, 1991: 626.

Type species. *Phoxocephalus holbolli* Kroyer 1842, selected by Boeck, 1876.

Diagnosis: Rostrum unstricted. Pigmented eyes lacking or vestigial in both males and females. Antenna 1 & 2 slender, weakly armed; flagella (in male) lacking calceoli.

Mandibular molar small but tritulative, palp lacking basofacial setae, apically strongly setose. Maxilla 1, inner plate bare.

Key to North American Pacific Genera of Phoxocephalinae

(after Barnard & Karaman, 1991: 592)

1. Mandibular molar reduced but triturative; peraeopod 7 (male), segment 5 little modified 2.
—Mandibular molar weak, non-triturative apex bearing spines; peraeopod 7 (male), segment 5, anterior margin with conspicuously modified, copulatory spines 3.
2. Eyes unpigmented or lacking (both sexes); gnathopods typically subsimilar in form and size.
. *Phoxocephalus* (p. 115)
—Eyes pigmented, distinct; gnathopod 2 usually larger than gnathopod 1 . . . *Cephalophoxoides* (p. 116)
3. Gnathopods either both subchelate or both parachelate; peraeopod 7 (male), segment 5, anterior copulatory spines are short, widely spaced, tips little modified *Metaphoxus* (p. 117)
—Gnathopod 1 slightly parachelate, gnathopod 2 subchelate; peraeopod 7 (male), segment 5 anterior copulatory spines are large, closely spaced, with strongly modified tips . . . *Parametaphoxus* (p. 121)

Coxae 1-4 setose postero-distally. Gnathopods subequal, medium, obliquely subchelate, carpus cryptic or nearly so. Peraeopods 3 & 4 stout, segment 5 spine elongate; dactyls small. Peraeopod 5, basis broad, segments 4 & 5 not expanded. Peraeopod 7 (male), segment 5 little modified as a clasping organ.

Pleon plate 3 large, margins lacking setae. Uropods 1 & 2 not powerful, rami marginally spinose.

Telson lobes long, narrowing distally, apex with single spine.

Taxonomic Commentary: According to Barnard & Karaman (1991), the genus *Phoxocephalus* is not now represented in the North American Pacific region. *Phoxocephalus homilis* J. L. Barnard, 1960, and a number of species from the southern hemisphere, have been removed to *Cephalophoxoides*. *Metaphoxus fultoni* (J. L. Barnard) had previously been removed by Gurjanova to the genus *Parametaphoxus*, and its representative on the N. American Pacific coast is here renamed *Parametaphoxus quaylei*, new species (see p. 121). We may note that *Metaphoxus frequens* J. L. Barnard of this subfamily is here retained within the genus *Metaphoxus* (p. 117). The present authors here provide evidence that supports this major subdivision of the genus *Phoxocephalus* by Gurjanova (1977) and by Barnard and Karaman (1991). The genus *Phoxocephalus* thus reverts to monotypy, containing only its original type species *P. holbolli* Kroyer.

Cephalophoxoides Gurjanova

Cephalophoxoides Gurjanova 1977: 81.—Barnard & Karaman, 1991: 602.

Type Species. *Phoxocephalus bassi* Stebbing, 1888.

Species (North Pacific Region): *Cephalophoxoides homilis* (J. L. Barnard, 1960); *C. proluxus* (Hirayama, 1987)?

Diagnosis: Rostrum unconstricted. Pigmented eyes well developed. Antennae short (female). Antenna 2 (male), peduncular segment 5 weakly calceolate, flagellum elongate, calceolate.

Mandibular molar triturative; palp segment 3 much shorter than 2. Maxilla 1, outer plate 7-spinose; palp 1-segmented. Maxilliped, plates small, weakly armed; inner plate with apical spine(s).

Coxae 1-4 large, deep, setose below. Gnathopods large, subchelate, propods unequal in size, 2 enlarged; carpus short, hind lobes cryptic.

Peraeopods 3 & 4 stout, dactyls long. Peraeopod 5, basis very broad; segments 4 & 5 not expanded. Peraeopod 6 elongate, segments 4-6 slender; dactyl long. Peraeopod 7, basis very broad, hind margin not dentate; dactyl long; segment 5 (male) not modified, or equipped with copulatory spines.

Pleon plate 3 large, margins smooth. Uropods 1 & 2, inner rami marginally spinose. Uropod 1, outer ramus shorter than inner. Uropod 3, fully setose, aequiramous in male, non-setose but sub-aequiramous in female; terminal segment of outer ramus elongate. Telson lobes with single apical spine. Coxal gill on peraeopod 7 small.

Taxonomic-biogeographical Commentary: "*Phoxocephalus*" *prolixus* Hirayama, 1987, from the Ariake Sea, Japan, has fully pigmented eyes in both sexes, and is here tentatively assigned to the genus *Cephalophoxoides*. However, it differs markedly from the eastern Pacific species, *C. homilis*, in having a smaller triturating molar surface, gnathopod propods subequal in size, and possessing an elongated meral process in gnathopod 2, among other differences.

Both North Pacific species differ markedly from counterparts in the southern hemisphere, assigned by Barnard & Karaman (1991) to the genus *Cephalophoxoides*, of which the type species is *C. bassi* (Stebbing). The northern forms may eventually merit separate generic recognition.

Cephalophoxoides homilis (J. L. Barnard)

(Fig. 26).

Phoxocephalus homilis J. L. Barnard, 1960: 370.

Cephalophoxoides homilis Gurjanova, 1977:81.—Barnard & Karaman, 1991: 603.

Material Examined:

BRITISH COLUMBIA: Southern mainland region: Jervis Inlet, ELB Stn. P2, 360 m. fine mud, Nov. 2, 1977, - 1 female. Howe Sound, C. Levings coll., Nov. 2, 1976 - 1 male penult. (4.5 mm), with slide mount (fig'd). CMN Cat. No. NMCC1992-1116, female (2.25 mm). Off Passage I., Howe Sound, ELB Stn. V6, 160 m., July 5, 1978 - 1 female; West Bay, ELB Stn. P2, 25 m., Nov. 2, 1977 - 1 female ov. Southern Vancouver Island: Off McCauley Pt., G. W. O'Connell coll., 61 m., Aug. 26, 1976 - 4 females.

WASHINGTON: San Juan Channel, 80-90 m., K. E. Conlan coll., Jan. 1, 1987 - 1 female ov. Off Brown Island, 55-60 m., Nov. 3, 1983, ELB coll. - 1 female ov. (3.5 mm), with slide mount (fig.'d), 2 im. females. CMN Cat. No. NMCC1992-1117.

Diagnosis: Female ov. (3.5 mm): Eyes medium large, round. Antennae short. Antenna 1, flagellum 5-segmented; accessory flagellum 3-segmented. Antenna 2, peduncular segments 4 & 5, hind margin with fan of long setae; flagellum 4-segmented.

Mandible, left lacinia 4-dentate, right lacinia flabellate; spine row short (2-5 blades). Maxilla 1, inner plate 7-spinose; palp indistinctly 1-segmented. Maxilliped, outer plate short, with 4 short inner marginal spines.

Coxa 1 broadening distally, margin with 7-8 setae. Coxa 4 very broad, hind margin convex. Gnathopod propods large, unequal (2 larger), hind margin of carpus with single cluster of setae.

Peraeopods 3 & 4, postero-distal spine of segment 5 slender, length = segment 6; segment 6 with a few postero-distal spines; dactyls slender. Peraeopod 5, basis very broadly rounded behind. Peraeopod 6, segment 4 weakly spinose; dactyl long, ~ 2/3 segment 6.

Pleon 3, hind margin with slight notch but no setae. Uropod 1, outer ramus shorter than inner, marginally bare; inner ramus with long marginal spines. Uropod 2, outer ramus with 3-4 slender marginal spines. Uropod 3, peduncular distal fan of spines weak; outer ramus, margins nearly bare; terminal segment slender, half length of proximal segment; inner ramus ~ 1/2 length of outer ramus.

Telson, apices each with single long spine and plumose setule; dorsal penicillate setae large, long.

Male penult. (4.5 mm): Eyes large, vertically oval. Antenna 2, peduncle 4 with weak brush setae; flagellum with 30+ short segments. Peraeopod 7, segment 5. Uropod 3, inner ramus as long as proximal segment of outer ramus.

Taxonomic and Distributional Commentary: The species ranges from southern Vancouver Island to southern California, in depths of 40-600 m, shallower in the north. The northern material is virtually identical with that from California described and figured originally by Barnard (1960, pls. 49-50).

Cephalophoxoides homilis differs rather markedly from the type species and other species of the Australian antipodean region (see generic commentary, above).

Metaphoxus Bonnier

Metaphoxus Bonnier, 1896: 630.—Barnard, 1960: 379 (partim).—Barnard, 1969: 419 (partim).—Gurjanova, 1951: 363 (key).—Barnard & Karaman, 1991: 621.

Type species: *Metaphoxus typicus* Bonnier, 1896 (= *Metaphoxus simplex* (Bate, 1857)).

Species (North American Pacific): *Metaphoxus frequens* Barnard, 1960 [379].

Diagnosis: Eyes pigmented (both sexes). Antenna (female) very short. Antenna 1 (male), proximal 3 segments calceolate. Antenna 2 (male), segment 5 with 2 anterior marginal calceoli, flagellum elongate, proximal segments calceolate.

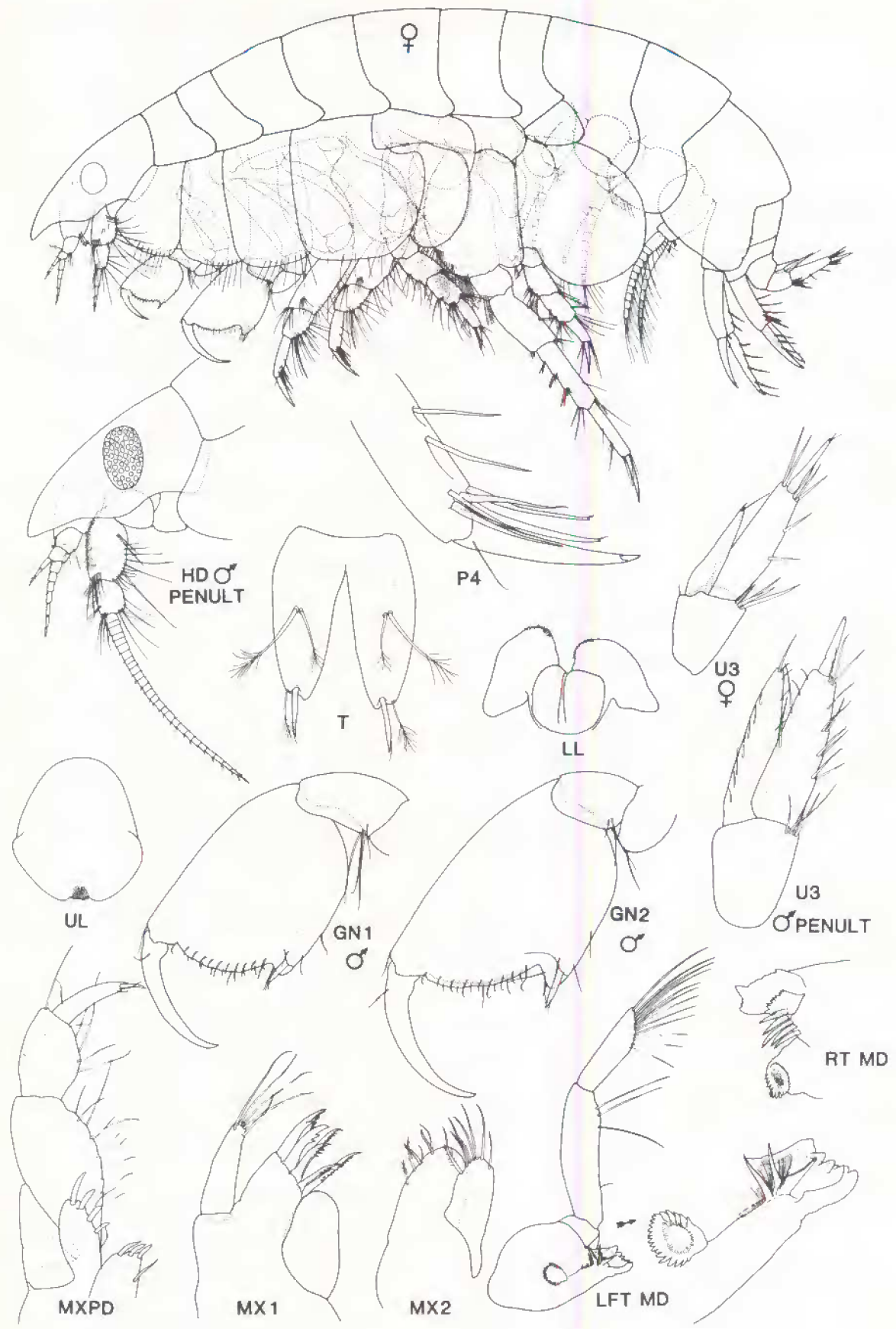
Mouthparts modified. Mandible, molar small, non triturative, with 2-3 apical blades; spine row short, blades thick, powerful; right lacinia flabellate, left lacinia unevenly denticulate; palp segment 3 expanded and truncate distally. Maxilla 1, inner plate lacking distal setae; palp sparsely setose. Maxilla 2, plates small, weakly setose. Maxilliped, inner plate tall, with single apical spine; inner plate small, slender very weakly armed.

Coxae 1-4 broad, deep, postero-distal margins with setal cluster. Gnathopods powerfully subchelate, propods unequal in size and form, gnathopod 2 the larger; carpus short, hind lobe cryptic.

Peraeopods 3 & 4 medium, weakly spinose & setose behind; dactyls slender. Peraeopods 5-7, bases very broad. Peraeopod 5, segments 4 & 5 not expanded. Peraeopod 6, anterior margin of basis strongly long-setose; segments 4-6 slender, weakly armed; dactyl small. Peraeopod 7 (female), basis very broad, hind margin smooth; segment 6 short; in male, anterior margin of segment 5 not incised, but armed with singly spaced stout spines, tips slightly bent and pectinate.

Pleon plate 3 rounded, margins bare or weakly setose. Uropod 1 lacking inter-ramal or displaced spines; rami subequal. Uropod 3 (female) inaequiramous, margins lacking setae. Telson lobes slender, elongate, apical spines elongate.

FIG. 26. *Cephalophoxoides homilis* (J. L. Barnard)
FEMALE ov. (3.5 mm); MALE (4.5 mm)
(SEE PAGE 118)



Taxonomic Commentary: This genus is very little different from *Parametaphoxus* Gurjanova, 1977. Aside from differences in the gnathopods, another major character of significance is the form of the copulatory spines on segment 5 of pereopod 7 (male). In males of the Mediterranean *M. simplex* Bate, Karaman (1993, p. 658) noted: "pereopod 7, carpus, anterior margin with 3-4 stout spines", but did not use the information in analysis of species relationships.

Distributional Commentary: The five species of the genus occur in littoral marine shallows, from the tide lines to depths of 458 m. in the northeastern Pacific, from 0-80 m. in the northeastern Atlantic, and from 0-48 m. in southeastern Australia. Such a widely disjunct distribution of component species suggests that the generic concept may be artificial, and held together by homoplasies, rather than by true synapomorphies.

Metaphoxus frequens Barnard
(Fig. 27)

Metaphoxus frequens Barnard, 1960: 379, Pl. 51.—Barnard, 1975: 341, fig. 161.—Gurjanova, 1977: 80.—Austin, 1985: 598.

Material Examined:

ALASKA: Leo Anchorage, ELB Stn. A165, July, 1961 - 3 females.

BRITISH COLUMBIA: North-Central coast: Open Bight, ELB Stn. H37, July 22, 1964 - 1 female ov. (2.5 mm), with slide mount (fig'd), 2 other females, 1 subadult male. CMN Cat. No. NMCC1993-0053. Off Kennedy I., 20 ft. depth, May 15/64 - 1 female; Ocean Falls, C. Levings Stn. 51B-04 - 3 females; Stn. 51B-38 - 1 female; Swanson Bay, C. Levings Stn. 51B-008 - 1 male, subadult.; Stn. 51B-004 - 2 specimens.

Vancouver Island: Port Hardy, ELB Stn. V6, July 22, 1959 - 1 female; Trevor Channel, ELB Stn. B14, May 25, 1977 - 1 female ov. (3.25 mm), with slide mount, 1 male penult., with slide mount; Ibid, lot 2 - 1 female. Broken Id., ELB Stn. B7, June 27, 1976 - 1 female. ELB Stn. P13, Trevor Channel, July 29, 1975 - 1 male, 1 female; ELB Stn. P26, Koprino Hbr., Aug. 14, 1975 - 2 males, 2 females.

French Creek, near Nanaimo, P. O'Rourke Stations, August 13-28, 1977: FC2 - 2; FC5 - 1 mature male, with slide mount (fig'd), CMN Cat. No. NMCC1993-0054; FC6 - 1 male penult.; FC7 - 1; FC13 - 1.

Sidney Channel, D.V. Ellis Stn. 1001, 1979 - 1 specimen. Shelf off Vancouver Island, Institute of Ocean Sciences, 1990: 14 stns (A4, A8, to 2C4) - 14 specimens, including juveniles, mature males, and females (ov.).

Diagnosis: Female ov. (2.5 mm): Rostrum long, reaching base of flagellum of antenna 1. Eye small, oval, weakly pigmented; Antenna 1, segments 2 & 3 very short; flagellum 4-segmented, accessory flagellum 2-3 segmented. Antenna 2, peduncular segment 4 with single facial cluster of slender

spines, hind margin sparsely long-setose; flagellum 4-5 segmented.

Mouthparts nearly typical of the genus. Mandibular palp segment 3 shorter than segment 2, tip expanded and subtruncate. Maxilla 1, inner plate large, margins bare. Maxilliped, inner plate columnar, with single apical slender spine; palp, dactyl heavy, nearly equal in length to segment 3.

Coxa 1 somewhat hatchet-shaped, hind corner with cluster of 6-7 setae. Coxa 4 very large, hind margin steeply convex. Gnathopod 1, propod smaller but more elongate, and palm less oblique, than in gnathopod 2.

Pereopods 3 & 4, postero-distal spine of segment 5 very slender, longer than segment 6; hind margin of segment 6 with single slender spine at mid-point; dactyls slender. Pereopod 5, basis extremely broad, hind margin convex. Pereopod 6, basis very broad, hind margin straight; segment 4, margins bare. Pereopod 7, basis very broad, orbicular, hind margin nearly smooth; segment 6 and dactyl short.

Pleon plate 3, hind margins with few very weak setae. Uropods 1 & 2, rami subequal, with 1 marginal spine. Uropod 3, rami bare; inner ramus short, < 1/2 outer ramus. Telson lobes narrowing distally, apical spines elongate, slender, tips curved. Coxal gills relatively small on pereopods 2, very small on pereopods 6 & 7.

Male (3.0 mm): Eye large, rounded, anterior ommatidia prominent. Antenna 1, peduncle 1 with strong posterior marginal brush setae; proximal 3 flagellar segments calceolate; antenna 2, peduncular segment 5 with 2 large anterior marginal calceoli; flagellum elongate, segments calceolate, distally alternately.

Pereopod 7, basis less broad than in female, hind margin with 3 small teeth; segment 5, anterior margin gently convex, armed with 3-4 well spaced, bent-tipped spines.

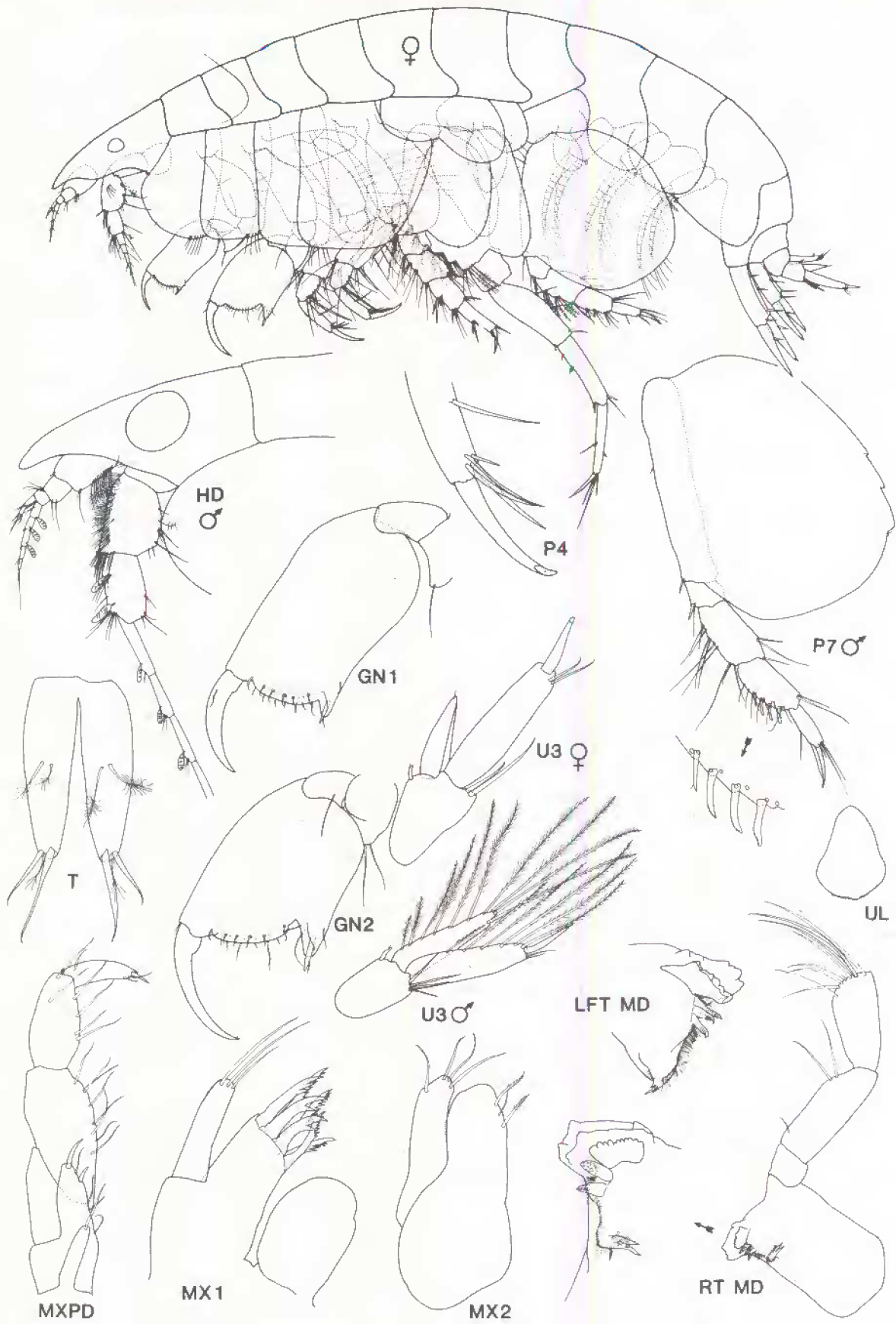
Uropod 3 inaequiramous; inner ramus 2/3 length of outer ramus; inner margins of rami plumose-setose; terminal segment, long, slender, bare.

Telson lobes slender, apices each with pair of long, slender spines

Distribution: This wide-ranging species occurs in the shallow subtidal from southeastern Alaska, through British Columbia and the northeastern United States, to southern California.

Taxonomic Commentary: The northern material compares closely in nearly all details with that described originally from California. In B. C. material, the palp of maxilla 1 is somewhat larger and margins subparallel. This species differs rather widely from its Australian counterpart species, and its higher level classification should be reexamined.

FIG. 27. *Metaphoxus frequens* J. L. Barnard, 1960. FEMALE ov. (2.5 mm); MALE (3.0 mm). Open Bight, B. C. (SEE PAGE 120)



Metaphoxus Barnard, 1960: 304 (partim).—Barnard, 1969: 419 (partim).—Lincoln, 1979: 364 (partim?).
Parametaphoxus Gurjanova, 1977: 81 (partim).—Barnard and Karaman, 1991: 624 (partim).

Type Species. *Parametaphoxus quaylei*, new species

Additional Species: *Parametaphoxus asiaensis* (Hirayama, 1992)[127].

Diagnosis: Very close to *Metaphoxus* Bonnier, but differing mainly in the form of the gnathopods (Barnard & Karaman, *loc. cit.*). In *Metaphoxus fultoni* (Scott) (designated type of *Parametaphoxus*, as illustrated by Lincoln, 1979: 367), the palm of gnathopod 1 is parachelate and the posterior lobe of the carpus is free, whereas in gnathopod 2, the palm is nearly vertical, and the posterior lobe of the carpus is evanescent and cryptic.

Female: Rostrum short. Pigmented eyes present. Antennae short.

Mandible, molar non-tritulative, apex with 0-1 blade-spines; spine row short left lacinia unevenly 5-6 dentate, right lacinia blade-like; palp segment 3 with truncate apex. Maxilla 1, inner plate irregularly shaped, palp short. Maxilla 2, outer plate small. Maxilliped, outer plate small, weakly spinose. Coxae 1-4 deep, lower hind corners weakly setose. Gnathopods powerful, propods somewhat dissimilar in form and size, 1 smaller but longer, and palm somewhat parachelate, rather than vertical or truncate; carpus of 1 elongate, shallow, "semi-eusiroidean" in form.

Peraeopods 3 & 4 moderate, hind margin of segment 6 nearly bare. Peraeopod 5, hind lobe of coxa deep, basis very broad; segments 4 & 5 narrow. Peraeopod 6, basis very large, deeply lobate; distal segments slender, elongate. Peraeopod 7, basis extremely large, subtriangular.

Pleon plate 3 ordinary, unarmed. Uropods 1 & 2, rami subequal, weakly armed. Uropod 3 small, margins nearly bare, inner ramus short. Telson lobes slender elongate (length > 3X width), apices with 2 spines. Coxal gills relatively small, sac-like on peraeopods 2-6, minute or lacking on peraeopod 7.

Male: Antenna 1, flagellum calceolate. Antenna 2, peduncle 5 with 2 calceoli; flagellum elongate, segments calceolate. Peraeopod 7, segment 5, anterior margin incised, with close-set, copulatory spines. Uropod 3, rami unequal, margins weakly plumose-setose.

Taxonomic and Distributional Commentary: The genus, as here defined, is restricted to the North Pacific region, including the Sea of Japan in the west, and in the east from British Columbia to southern California. The type of Gurjanova's genus *Parametaphoxus* was based on *Metaphoxus fultoni* (Scott, 1890). The latter is an eastern Atlantic species having the same form of male peraeopod

KEY TO KNOWN SPECIES OF PARAMETAPHOXUS

1. Basis, hind margin with 3 small teeth; antenna 1, flagellum 4-5 segmented; gnathopod 2, propod distinctly longer than deep *P. quaylei* n. sp. (p. 121)

—Basis, hind margin with 5 distinct teeth; antenna 1, flagellum very short, 3-4 segmented; gnathopod 2, propod about as deep as long, squarish *P. asiaensis* (Hirayama)

copulatory apparatus as in *M. frequens* and other members of the genus *Metaphoxus* (e.g. *M. pectinatus*, Walker). However, the species from the N. American Pacific region, formerly identified as *M. fultoni*, has a different type of copulatory apparatus than that of the eastern Atlantic TYPE of *M. fultoni*. Thus, the eastern Pacific form is a distinctly different species (newly named *P. quaylei* below). Since Gurjanova (1977) was referring to the eastern Pacific form of "*M. fultoni*", that form becomes the type of her valid new genus, *Parametaphoxus*. *Metaphoxus* was originally described from the N. Atlantic, based on *M. typicus* Bonnier. It includes also *M. chelatus* (Calman, 1896) and several others from the Mediterranean and northeastern Atlantic region (Barnard & Karaman, 1991, p. 622).

Parametaphoxus quaylei new species
(Fig. 28)

Metaphoxus fultoni: Barnard, 1960: 304, plate. 18.—Barnard, 1975: 361, fig. 162.

Parametaphoxus fultoni Barnard & Karaman, 1991: 625 (partim)?

Material Examined:

BRITISH COLUMBIA: North-Central Coast: Rennison Island, ELB Stn. H30, 8-25 m., July 20, 1964 - 3 females, 1 juv.; Banks I., ELB Stn. H21, July 17, 1964 - 1 female. Ocean Falls, C. Levings Sta. 24B-009, 100 m., 1972 - 1 male; Swanson Bay, C. Levings Sta. 51B-031, 25 m., April 4, 1973

1 male; *ibid.*, Sta. 51B-008, 66 m., Nov. 18, 1975 - 1 adult male, with slide mount.

Southern Vancouver Island: Berkeley Sound, Diana I, ELB Stn. B26, July 8, 1976 - 1 female; Off McCauley Pt., Victoria, G. O'Connell coll., 27 m., Aug. 26, 1976 - 1 female ov. (2.5 mm), with slide mount, + 1 other female. Off Clover Pt., Victoria, G. O'Connell, Aug. 28, 1976, 41 m. - 3 females. Saanich Inlet, K. E. Conlan coll., Jan. 16, 1976 - 1 female ov. (2.5 mm), HOLOTYPE, with slide mount, CMN Cat. No. NMCC1993-0050; 1 adult male (2.75 mm), ALLOTYPE, with slide mount, CMN Cat. No. NMCC1993-0051; 5 males, 7 females, PARATYPES, CMN Cat. No. NMCC1993-0052. D.V. Ellis Stns., 1979: Sidney Channel, Stn. 1001 - 2 specimens; Boatswain Bank, Stn. 1601-2-8 specimens; Haro Strait, Stn. 2202 - 1 specimen.

WASHINGTON: Brown Bay, San Juan Co., 50-60 m., ELB colln., Nov. 9, 1983 - 2 females.

Diagnosis: Female ov. (2.5 mm): With the characters of the genus. Differing from *P. asiaensis* by the character states of the key (above) and the following: Eyes medium round. Antenna 1, flagellum 4-5 segmented; accessory flagellum 3-segmented. Antenna 2, peduncular segment 4 with facial cluster of 2 spines; segment 5 short, with single anterior marginal and distal spine groups; flagellum 4-5-segmented.

Mandible, spine rows with 2-3 short thick heavy blades; palp segment 3 nearly equal in length to segment 2, with single long baso-facial seta. Maxilla 1, palp with 3 apical setae. Maxilla 2, plates apically with 3 setae. Maxilliped, outer plate with 1 apical spine; palp, dactyl weak.

Coxae 1 & 2 little broadening distally, lower posterior margin with 6-8 setae; coxa 4 very deep, hind margin nearly vertical. Gnathopod 1, propod longer than deep, slightly parachelate; carpus hind lobe with single setae. Gnathopod 2, propod rectangular, palm perpendicular, carpus with cryptic hind lobe.

Peraeopod 5, basis very broad, strongly rounded behind. peraeopod 6 very large, long; basis narrowing distally to large lobe, hind margin nearly straight; segments 4-6 slender, margins nearly bare; peraeopod 7, hind margin with 2-3 weak teeth; segment 5 short.

Pleon plate 3, hind corner produced, subquadrate, margins bare. Uropods 1 & 2, rami with 0-2 weak marginal spines. Uropod 3, terminal segment of outer ramus of medium length, < 1/2 proximal segment.

Telson, apex of each lobe with pair of unequal spines.

Male (2.75 mm): Pigmented eyes large, sub-orbicular. Antenna 1, proximal 3 flagellar segments calceolate. Antenna 2, peduncular segment 4 strongly brush-setose; peduncle 5 with 2 antero-distal calceoli; flagellum elongate, segments calceolate, distally alternately. Peraeopod 5, segment 5, anterior margin with 3 close-set, elongate, apically clavate copulatory spines and a single shorter spine. Uropod 3, rami with distal plumose setae.

Etymology: Named in honour of the late Dr. D. B. (Dan) Quayle, Nanaimo, British Columbia, whose life-long work in marine biology has contributed greatly to knowledge of invertebrate animals of the North American coastal marine region.

Taxonomic Commentary: In material of *Parametaphoxus* from the North American Pacific coast (represented by the present material from British Columbia, and by material from California formerly identified as *Metaphoxus fultoni* (Scott) by J. L. Barnard (*loc. cit.*), the condition of the gnathopods is closely similar to that of *M. fultoni* (Scott) from the European Atlantic region. However, in Pacific regional males, the anterior margin of segment 5, peraeopod 7, is slightly incised, and the protruding copulatory spines are relatively long, close-set, and bear complexly expanded tips. In European Atlantic males (as illustrated by Lincoln (*loc. cit.*)), the anterior margin of segment 5 is gently convex, and

the 3 copulatory spines are relatively short, simple, and widely spaced. Therefore, on the basis of this major character difference, and on lesser differences noted in the diagnosis above, the present species is considered distinct from *Parametaphoxus fultoni* (Scott) from the European Atlantic region and is herewith described as *P. quaylei*, new species.

The material described and figured by Barnard (1960, *loc. cit.*) is closely similar to the present northern species, esp. in the unique form of the gnathopods. However, the female of Barnard's material is slightly larger (3.0 mm), has larger pigmented eyes, coxa 1 is anteriorly subacute, coxa 5 has a very deep rounded posterior lobe, the basis of peraeopod 5 is irregularly rounded behind, and the basis of peraeopod 6 has an acute postero-distal lobe, etc. Regretably, the form of the copulatory spines of the male of the southern form have not yet been described. Such information is needed to elucidate the taxonomic value of the other character state differences noted above.

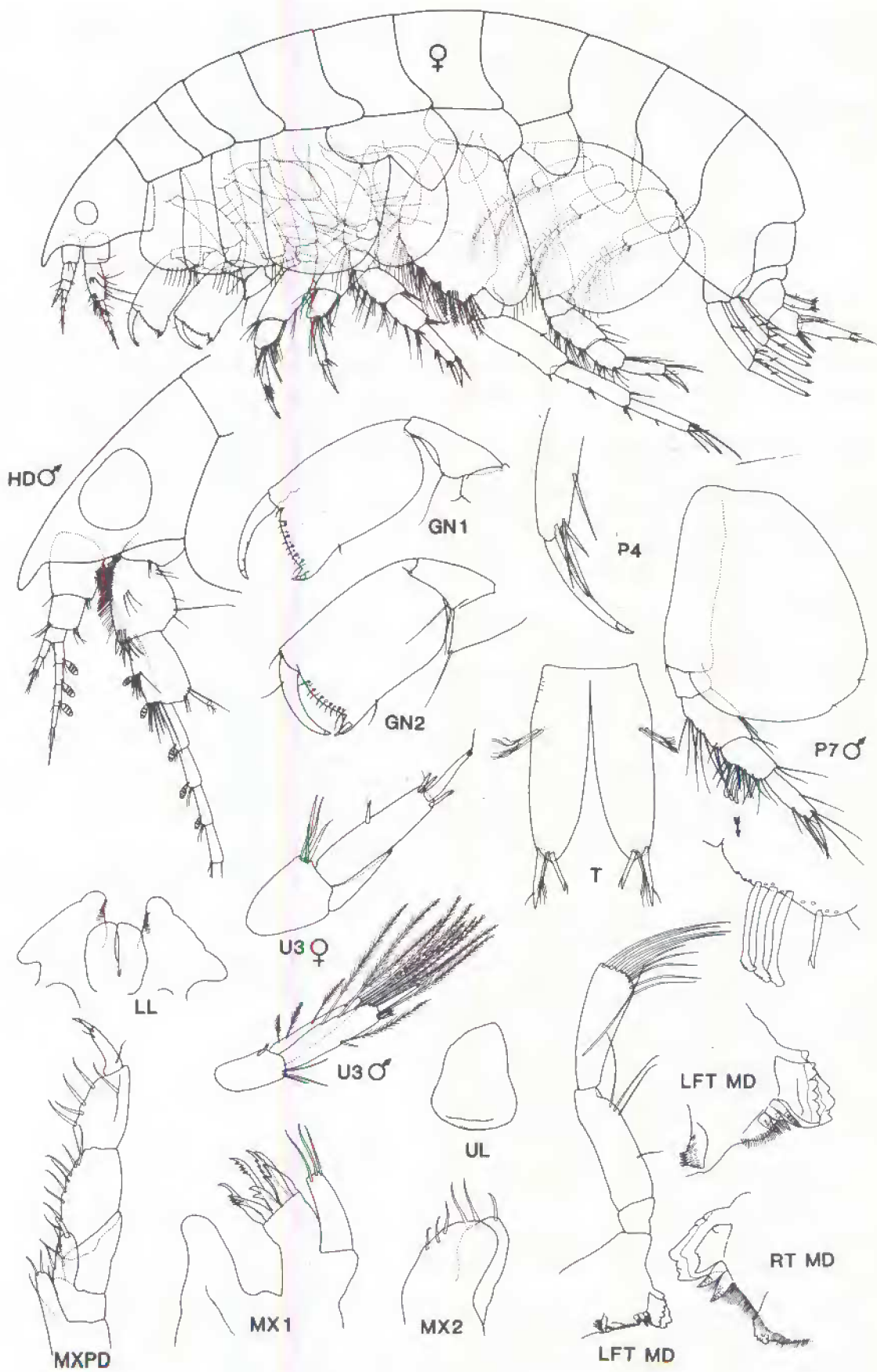
Distribution: Known only from British Columbia and Washington State, subtidally in coastal waters, in depths of 25-50 m, ranging to more than 100 m. in depth.

Parametaphoxus asiaensis (Hirayama, 1992)

Metaphoxus fultoni Hirayama, 1987: 58, figs. 260-263.
Metaphoxus fultoni asiaensis Hirayama, 1992: 127, figs. 10-14.

Taxonomic Commentary: The material ascribed by Hirayama (1987) to *Metaphoxus fultoni* (Scott) of the N. Atlantic region is clearly much more similar to the N. American Pacific form, *Parametaphoxus quaylei*, new species (above). Hirayama's specimen (2.5 mm) was labelled as a male in figs. 260-262, but is certainly an adult female, since a brood plate is shown on peraeopod 1, the pigmented eye is small, antenna 2 is short, and peraeopod 7, segment 5, is unmodified. This specimen differs from females of the North American species, however, in the smaller, shorter antennae, less slender gnathopod 2, and in the different form and margination of the basis of peraeopod 7, among other features. Hirayama (1992, p. 127) has since merged the Japanese material with that from Hong Kong as a new species of *Metaphoxus*, *M. fultoni asiaensis* Hirayama. Hirayama did not figure the copulatory apparatus of peraeopod 7 of mature males in any of his material, but on general taxonomic grounds we presume it to be similar in generic form to that of *P. quaylei*. For reasons given above, we here transfer Hirayama's name to the genus *Parametaphoxus*, and elevate it to full species status, as *Parametaphoxus asiaensis*. (Hirayama, 1992).

FIG. 28. *Parametaphoxus quaylei*, new species.
FEMALE ov. (2.5 mm) HOLOTYPE; Male (2.75 mm)
ALLOTYPE (SEE PAGE 123 - OPPOSITE)



Distribution: Japan Sea; South central Japan and coast of North Korea, to Hong Kong. The disjunct distribution of species within the genus *Parametaphoxus* is typical of amphipacific warm-water taxa whose ranges have been probably been discontinuous since post-Miocene cooling took place.

HARPINIINAE Barnard & Drummond

Harpiniinae Barnard & Drummond, 1978: 528.—Barnard & Karaman, 1991: 591 (key).

Type Genus: *Harpinia* Boeck, 1872: 218.—Barnard & Karaman 1991: 611. (~20 species, only 2 in N. Pacific.)

Genera: (i) North American Pacific region:

Heterophoxus Shoemaker, 1925: 22; Barnard & Karaman, 1991 [613] (6 species, N. Pacific and S. African); *Harpiniopsis* Stephensen, 1925 [171]; Barnard & Karaman, 1991 [612] (20 spp., mostly N. Pacific, Indian Ocean); *Pseudharpinia* Schellenberg, 1931; Barnard & Karaman, 1991 [628] (13 species, mostly N. Pacific).

(ii) World-wide: *Feriharpinia* Barnard & Karaman, 1982 [183] (TYPE - *H. ferentaria* Gurjanova, 1977 (Okhotsk Sea and Kamchatka)); *Palabriaphoxus* Gurjanova, 1977 [74] (TYPE - *H. palabris* J.L. Barnard, 1961 (Tasman Sea, 610 m.); *Torridoharpinia* Barnard & Karaman, 1982 [184] (TYPE - *Proharpinia hurleyi* J. L. Barnard, 1958 (New Zealand, subantarctic islands); *Cocoharpinia* Karaman, 1980 [154] (TYPE - *C. iliffei* Karaman, 1980 (Bermuda sea caves); *Proharpinia* Schellenberg, 1931 [80], (TYPE - *P. antipoda* Schellenberg, 1931 (Magellanic to Madagascar).

Diagnosis: Rostrum fully hooded, not laterally incised; pigmented eyes lacking (except in *Heterophoxus*). Antennae (esp. peduncles) very short (always so in female). Antenna 1 (male) flagellum variously (usually weakly) callynophorate, rarely calceolate. Antenna 2, segment 1 weakly to strongly ensiform; in male, peduncle 5 distally calceolate; flagellum often elongate, basally calceolate.

Mouthparts: Mandible, molar weak, stubby, with apical blades; spine row short, thick; left lacinia 4-5 dentate; incisor not much broadened; palp slender, segment 1 relatively long. Maxilla 1, outer plate 7-11 spinose, palp 2-segmented. Maxilliped, plates small, inner with 0-1 apical spine; palp, dactyl small, unguis long.

Coxal plates, large, broad, lower margins with widely spaced plumose setae. Gnathopods medium subchelate, subsimilar, carpus short.

Peracopod 5, basis narrow (extreme case of pyriform shape of Pontoharpiniinae), distal segments short, sublinear; coxa, hind margin deep. Peracopod 6, basis pyriform, distal segments elongate. Peracopod 7, basis usually strongly

serrate or toothed behind; distal segments usually short; in the male, segment 5 unmodified, but dactyl often longer and more strongly curved than in the female..

Uropods 1 & 2, rami slender, weakly spinose behind. Uropod 3 inaequiramous (female), aequiramous (male). Telson, basally fused (1/10 - 1/3 of total length), slender-spinose.

Coxal gills sac-like, smallest on peraeopod 7. Brood plates ordinary.

Taxonomic-Distributional Commentary: This subfamily is well represented in the North Pacific region, by many of the more primitive and relatively shallow water taxa, including the genus *Heterophoxus* which Barnard & Karaman (1991, p. 613) place close to the ancestral harpiniin. The considerable degree of taxonomic diversity entrained within genera, particularly with respect to mouthpart morphology, suggests that further revisionary work is desirable. However, such a revision would necessarily be world-wide and beyond the scope of this study.

Harpinia Boeck

Harpinia: Boeck, 1876: 218.—Gurjanova, 1951: 365.—Barnard & Karaman, 1991: 611.

Taxonomic Commentary: Only two species, *H. antennaria* Meinert, 1893, and *H. pectinata* Sars, 1895, have been recorded from the North Pacific region, and these only from the northern (arctic) portion of the Bering Sea. Although the species are not treated here taxonomically, the following key may be used to distinguish them:

1. Peraeopod 7, hind margin of basis with 4-5 strong teeth; pleon plate 3 weakly produced, tooth little longer than basal width *H. pectinata* Sars

—Peraeopod 7, hind margin of basis normally serrate; pleon plate 3, tooth strongly produced, twice basal width *H. antennaria* Meinert

Heterophoxus Shoemaker

Heterophoxus Shoemaker, 1925: 22.—Barnard, 1960: 318.—Barnard & Karaman, 1991: 613.

Type species: *Heterophoxus pennatus* Shoemaker, 1925. (non *Harpinia oculata* Holmes, 1908).

Species (North American-Pacific): *Heterophoxus oculatus* (Holmes, 1908); *H. conlanae*, new species; *H. ellisi*, new species; *H. affinis* (Holmes, 1908); *H. pennatus* Shoemaker, 1925; *H. nitellus* Barnard, 1960; *Heterophoxus species* (part of Barnard, 1960, southern California).

KEY TO NORTHEASTERN PACIFIC GENERA OF HARPINIINAE
(partly after Barnard & Karaman, 1991: 591)

1. Pigmented eyes present (always in male); antenna 1 (male), flagellum calceolate, not callynophorate; antenna 2, peduncle 5 with 5-7 anterior marginal calceoli; telson broader than long. *Heterophoxus* (p.124)
—Eyes lacking or unpigmented (both sexes); antenna 1 (male) callynophorate, lacking calceoli; antenna 2 (male) peduncle 5 with 2 marginal calceoli; telson longer than broad 2.
2. Sexes strongly dimorphic; antenna 2 of male, flagellum elongate; antenna 1, male, basal flagellar callynophore weak 3.
—Sexes similar; antenna 2 of male short as in female; antenna 1, (male) flagellum with brushy basal callynophore *Harpinia* (p. 124)
3. Some rami of uropods 1-2 with posterior spines to apex; segment 2 of outer ramus of uropod 3 short; antenna 2, segment 1 usually ensiform *Pseudharpinia* (p.140)
—Uropod rami not spinose to apex; segment 2 of outer ramus of U3 elongate; antenna 1 weakly (or not) ensiform *Harpiniopsis* (p. 135)

Taxonomic Commentary: Holmes (1908) based his original descriptions of *H. oculus* and *H. affinis* on very limited material from off the Channel Islands in southern California. Barnard's subsequent more extensive work (1960) confirmed and extended the species complexity (variation).

The present northern material contains additional morphological and ecological complexity which may indicate some or all of the following possible explanations: (1) Holmes' original species are wide ranging and variable; (2) Holmes' and Barnard's descriptions mask the presence of other North American species; (3) Holmes' species do not extend north to Alaska, and other northern species may be included in the BC material.

Without re-examination of the original material of both Holmes and Barnard (loc. cit.), and without consistent application of several diagnostic taxonomic characters not treated or illustrated by Holmes or Barnard (loc. cit.), but newly recognized herein, such explanations remain enigmatic. However, possibility (3) may be the likeliest correct scenario in view of what has been shown to be probably correct with other species complexes within other phoxocephaloidean subfamilies of the North American Pacific region.

Diagnosis: (see basic diagnosis in Barnard & Karaman, above). Rostrum entire, unstricted. Eyes pigmented, sexually dimorphic. Antenna 1 (male), peduncle 1 posterodistally pseudocallynophorate (with cluster of fine aesthetascs); flagellum basally calceolate, not callynophorate. Antenna 2, segment 1 strongly ensiform; in male, flagellum elongate, calceolate; peduncular segment 5 with 5-7 anterior marginal calceoli.

Mouthparts: Mandibular molar not triturate, with marginal blades; palp slender; incisor not broadened, regularly

toothed. Maxilla 1, outer plate 9-spinose; palp broad, 2-segmented. Maxilla 2 weak. Maxilliped, inner plate setose, lacking apical spine(s); palp, dactyl short, with long apical spine.

Gnathopods, propods subsimilar, carpus of 1 with free hind margin. Peraeopod 5 short < peraeopod 7. Peraeopod 6 distal segments long. Peraeopod 7 (male), segment 5 unmodified but dactyl slender, curved forward.

Pleon plate 3, hind corner produced, lower margin setose. Uropods 1 & 2, outer ramus longer than inner. Uropod 2, outer ramus with special spines in some species. Uropod 3 variously inaequilateral, terminal segment of outer ramus minute; rami (male) marginally plumose-setose.

Telson lobes short, rounded, basally fused.

Taxonomic Remarks: Despite Barnard's re-examination of the type specimens of Holmes (1908) and Shoemaker (1925), the diversity of character states illustrated by Barnard (1960, plate 61) and his limited analysis of all characters states appears insufficient to justify synonymy of *oculus*, *pennatus*, and *affinis* under Holmes' original name *oculus*. Northern material differs significantly from Californian specimens in a number of character states involving the antennae, peraeopods, uropods, and pleon plate 3, for example. These differences are indicated in pertinent species descriptions, and in the key to North American Pacific species given below.

The South African species of *Heterophoxus* include the following: *Heterophoxus cephalodens* Griffiths, 1975; *H. opus* Griffiths, 1975; *H. ophthalmicus* (Schellenberg, 1925); and *H. trichosus* K. H. Barnard, 1932. These differ from North American counterparts mainly in having uropod 1 (and uropod 2?) with short bare outer ramus. The antarctic species, *H. videns* K. H. Barnard 1930, is similar to *H.*

KEY TO NORTH AMERICAN PACIFIC SPECIES OF *HETEROPHOXUS*

1. Peraeopod 6, segments 6, posterior marginal setae and/or spines lacking (or nearly so); telson lobes fused basally; pleon plate 3, hind process usually strong, upcurved 2.
 - Peraeopod 6, segment 6 with posterior marginal setae; telson lobes separated nearly to base; pleon plate 3, hind process short or medium, but nearly straight, not strongly upcurve. 5.
2. Peraeopod 6, segment 5 lacking posterior marginal spines or setae 3.
 - Peraeopod 6, segment 5 with posterior spines and setae 4.
3. Coxae 1 & 2, lower margins setose throughout; antenna 2 (male) peduncle 5 with 7 anterior marginal calceoli *H. affinis* (p. 126)
 - Coxae 1 & 2, lower margins setose posteriorly only; antenna 2(male), peduncle 5 with 5 marginal calceoli *H. pennatus* (p. 134)
4. Peraeopod 7, basis, hind margin normally toothed or serrate; pleon plate 3, hind process basally thick *H. nitellus* (p. 134)
 - Peraeopod 7, basis, hind margin strongly (deeply) toothed; pleon plate 3, hindprocess slender *Heterophoxus* sp. 1 (p. 134)
5. Peraeopod 6, segment 6 with singly inserted posterior marginal setae; pleon 3 with medium hook; peraeopod 7 (female) lacking coxal gill 6.
 - Peraeopod 6, segment 6 with doubly or triply inserted posterior marginal setae; pleon plate 3 with weak posterior process; peraeopod 7 (female) with small coxal gill 7.
6. Peraeopod 6, segment 5 with two short posterior marginal spines only; uropod 2 (male), spines not special; uropod 2, peduncular marginals very long *H. ellisi* n. sp. (p. 132)
 - Peraeopod 6, segment 5, posterior margin with at least one spine and setal cluster; uropod 2 (male), outer ramus with row of elongate copulating spines; uropod 2, spines normal . *H. ellisi* variant (p. 134)
7. Peraeopod 6, segment 6 distinctly longer than segment 5; hind margin with distal doubly inserted setae; pleon plate 3 lower margin with 20 setae; California *H. oculatus* (p.125)
 - Peraeopod 6, segment 6 barely longer than segment 5; hind margin with doubly and triply (not (or rarely) singly) inserted setae, pleon plate 3, lower margin with 7-10 marginal setae. *H. conlanae* n. sp. (p. 130)

Heterophoxus affinis (Holmes)
(Figs. 29A, 30)

Harpinia affinis Holmes, 1908: 523, fig. 29.

Heterophoxus oculatus Barnard, 1960, pl. 60: A - D. (WASH.);—pl. 60: L CAL., Velerio Stn. 2414);—pl. 61: G, H, I (CAL., Stn. 2170).

non: *Heterophoxus pennatus* Shoemaker, 1925: 22, figs. 1-3. (Gulf CAL).

Harpinia oculata Holmes, 1908: 521, fig. 28.—Barnard, 1960: 320, pl. 59 (= *Heterophoxus* sp. 1);—pl. 60, D-K;—pl. 61, J. (new).

Harpiniopsis oculatus nitellus Barnard, 1960, pl. 61: A-F.

Material Examined:

SE ALASKA: ELB Stns., 1961: Resurrection Bay, Stn. A135, 24 m., July 11 - 1 female ov. (9.0 mm), with slide mount; Leo Anchorage, Stn. A165, 40-50m, mud, July 23 - 6 females, 1 male; ibid., Stn. A167 - 1 female (variant).

FIG. 29A. *Heterophoxus affinis* (Holmes)
29B. *Heterophoxus oculatus* (Holmes)
(SEE PAGE 127 - OPPOSITE)

FIG. 30. *Heterophoxus affinis* (Holmes)
FEMALE (ov.) (7.0 mm); MALE (7..25 mm).
(SEE PAGE 128)

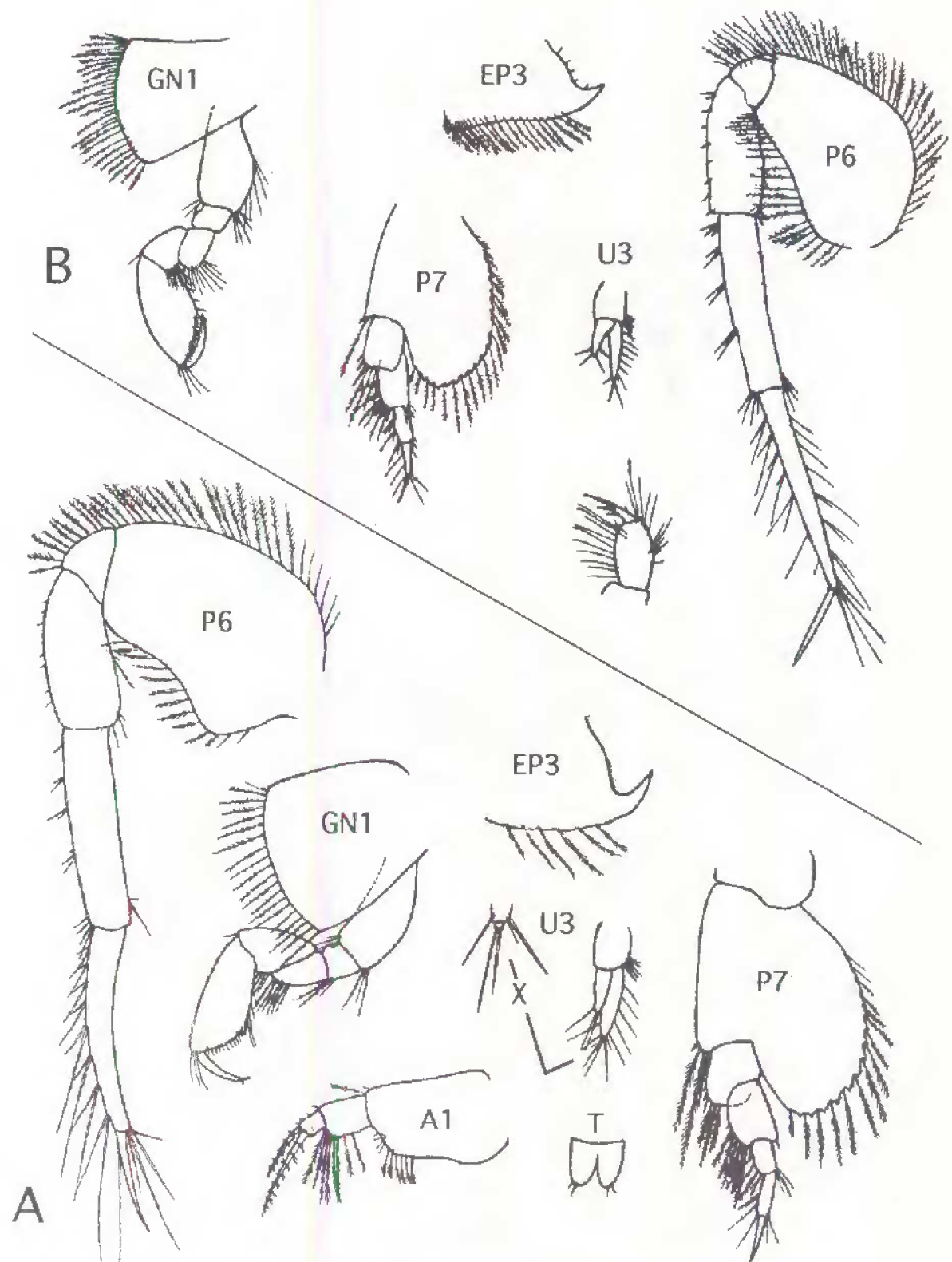
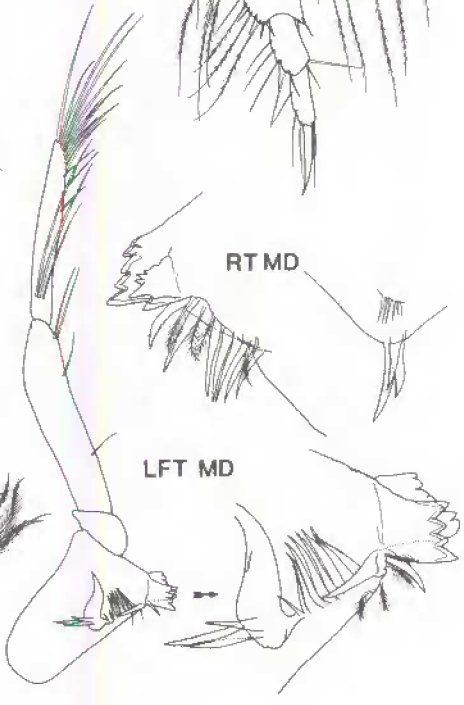
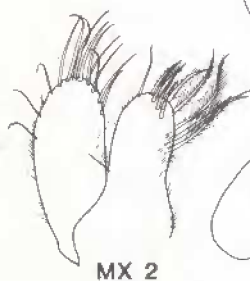
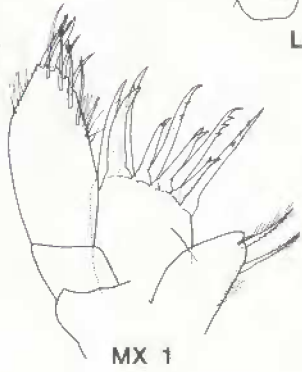
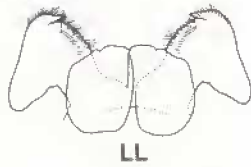
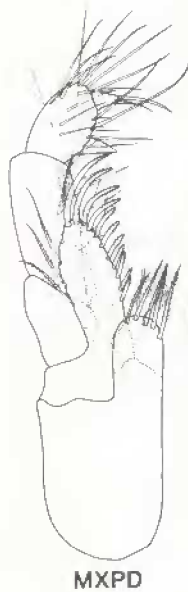
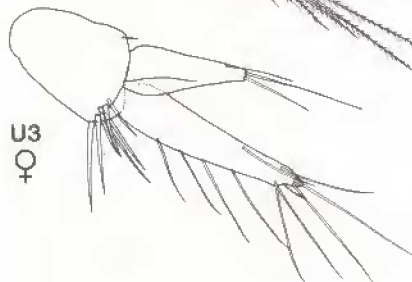
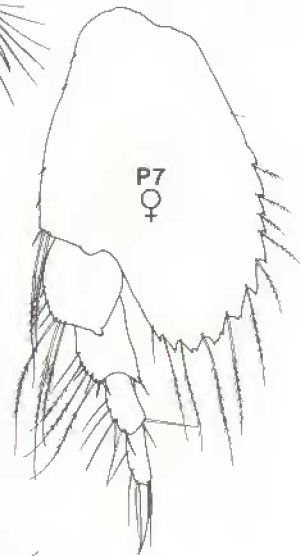
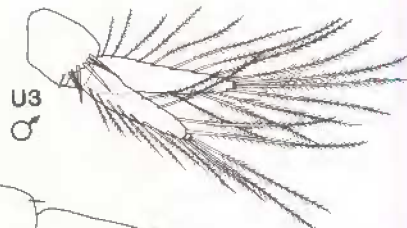
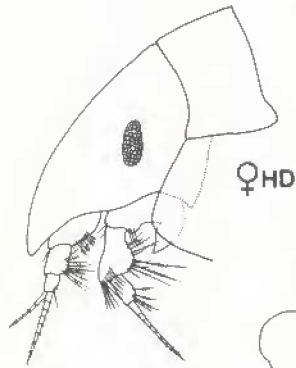
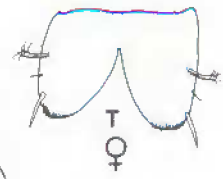
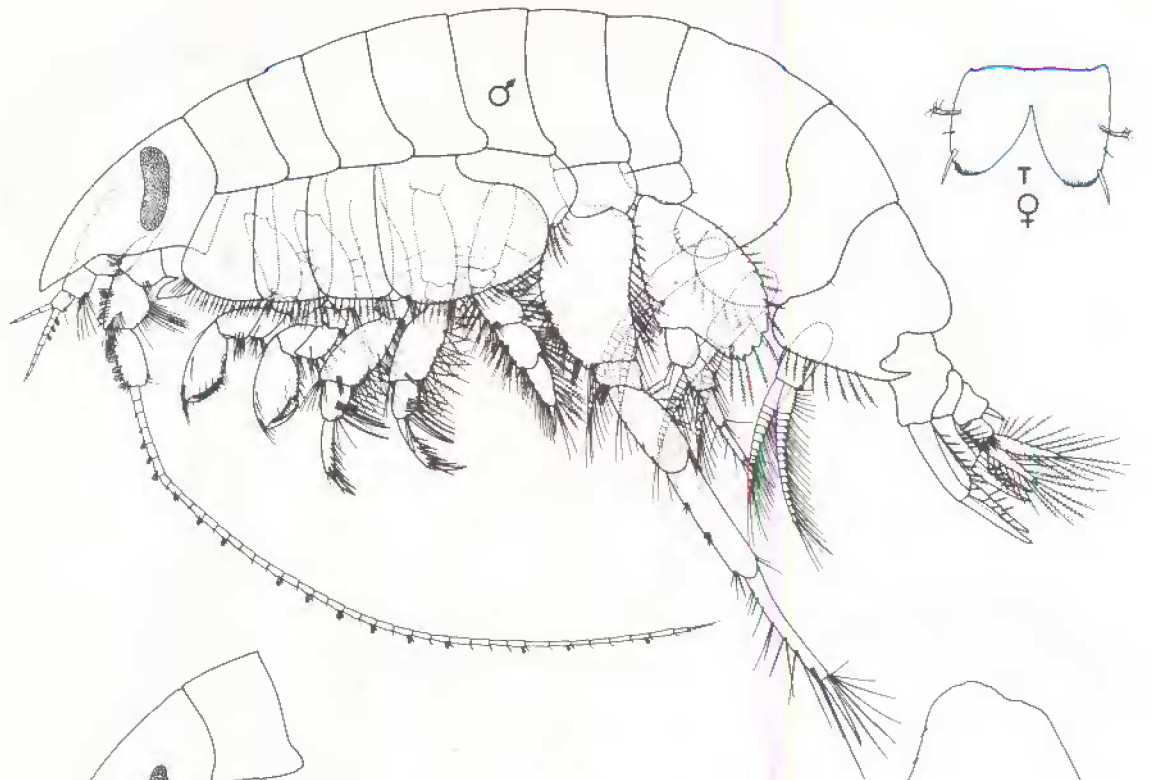


FIG. 29A. *Heterophoxus affinis* (Holmes). Female (9.0 mm). Monterrey Bay.

FIG. 29B. *Heterophoxus oculatus* (Holmes). Female (8.0 mm). Off South Coronado I.

(all figures modified from Holmes, 1908)



BRITISH COLUMBIA: Queen Charlotte Islands region: Dixon Entrance, J W Scoggan Stn. 105, 135 m., Aug. 12, 1965 - 2 females.

South-Central coast: ELB Stns. J1, Jervis Inlet, 360 m., mud, May 12, 1977 - 4 females, 8 juvs.; *Ibid.* J2, 576 m., - 15 specimens incl. males & females.

Burrard Inlet region: ELB Stns, Nov. 2, 1977: Stn. P4, 110 m., mud, (4 vials)- approx 100 specimens, incl. mature males, females, and immatures; Stn. P5, 80 m. (20); P6, 110 m. (40); Queen Charlotte Channel, St. P7, 240 m. - 1 male (7.5 mm), 1 female (7.0 mm); P8 (2 males, 2 females).

Pilot Cove, ELB Stn. P1, 44-50 m - 1 male (7.25 mm), 1 female ov. (7.0 mm), with slide mounts, + 15 other specimens. West Bay, Stn. P2, 20-24 m. (2 vials) - 87 specimens; Stn. P3, 60 m. (3 vials) - 1 female br. II (7.0 mm), with slide mount (fig'd), 1 male (7.5 mm), with slide mount (fig'd), + 40 specimens (males, females, juvs.) CMN Cat. No. NMCC1993-0040.

Burrard Inlet region, ELB Stns., July 4-5, 1978: V2, 3-8 m. - 3 females, 7 im.; V3, 25 m. - 10 specimens; V4, 50 m. - 40 mostly im.; V6, 160 m. - 60 specimens (males, females, im.). C. Levings Stns., Sept. 1, 1977: B1, 51 m. - 6 females; Stn. B4, 112 m. - 2 females, 2 im.; B6, 24 m. - 2 males, 8 females, 5 im.

Vancouver Island: Haro Strait, D V Ellis Stns. 2701-2702, 20 m., March 8, 1979 - 3 females.

Outer Shelf, IOC Stn. DS 405-1, (3 lots) - 12 specimens including mature males and females.

Numukamis Bay, PF and HB Stns A2112, - 1 female; ROM, J P Tully cruise, Jan. 23, 1988, - 1 male .

WASHINGTON: Friday Harbor, KE Conlan colln, 20 m., Jan 1, 1987, - 6 females.

Diagnosis. Female ov. (6.5 mm): Rostrum large, down-curved apically. Eye small, remote from lower head margin. Antenna 1, flagellum 8-9 segmented; accessory flagellum 4-5 segmented. Antenna 2, peduncle 4 with distal fan of 8 medium spines, segment 5 short; flagellum with 9-10 segments.

Mandible, molar, apex with 3 blades; spine row with 8 blades; left lacinia unevenly 7-dentate, right lacinia flabellate; palp segment 3 with 3 strong baso-facial setae. Maxilla 1, palp very broad. 1 apical spine distinctly largest. Maxilla 2, inner plate with 3 facial setae. Maxilliped, inner plate broad, 5 apical setae; outer palte with 11 strong curved masticatory spines; palp segments 2 & 3 relatively broad, heavy.

Coxae 1-4 medium deep, lower margin setose throughout. Coxa 4 little broader than deep, front corner rounded. Gnathopod 1, posterior margin of carpus long, ~1/2 anterior margin; propods relatively small.

Peraeopods 3 & 4, segment 5 short; segment 6 hind margin with 5-6 spine clusters; dactyl medium, length about 1/2 segment 6.

Peraeopod 5, coxa, hind lobe relatively small and shallow, depth less than proximal margin; dactyl short ~1/2 segment 6. Peraeopod 6, basis shallowly emarginate behind, with proximal marginal bulge; segments 5 & 6 medium long, hind margins devoid of spines and setae, anterior margin of segment 5 with 2 spine groups; dactyl medium. Peraeopod 7, basis, hind lobe narrow, margin with 9-10 strong teeth.

Pleon plate 3 with strong posterior upcurving hook or process, lower margin sloping upwards posteriorly, with 9-10 medium long setae. Uropods 1 & 2, rami with 3-4 medium spines. Uropod 2, peduncle with relatively few (6-7) long outer marginal spines. Uropod 3, outer margin of outer ramus with several slender non-plumose setae, inner ramus longer than peduncle.

Telson little longer than wide, lobes fused basally 1/4 to 1/3 their length.

Male (7.5 mm): Eye large, slender-reniform, nearly vertical. Antenna 1, peduncle 2 with postero-distal fan of 3-5 plumose setae; basal 3 flagellar segments calceolate. Antenna 2, peduncle 5 short, little longer than segment 4, anterior margin with 6-7 calceoli; flagellum with 35-40 segments, alternately calceolate.

Peraeopod 7, dactyl shorter than segment 6, slender, curved forwards.

Uropod 3, peduncle with distal fan of 4-5 spines; ramal margins with 4-9 plumose setae.

Taxonomic Commentary: Barnard (1960, *loc cit.*) partially figured a mature male of this species from Friday Harbor, WA., that agrees in nearly every detail with the present northern regional collections. Holmes' original illustration (Fig. 29A) clearly shows the posterior margin of segment 6 of peraeopod devoid of spines or setae in *H. affinis*. This contrasts with the single and double pairs of setae shown on that margin in his drawings of *H. oculatus* (Fig. 29B). The posterior tooth of epimeral plate 3 also contrasts strongly in the two species.

The Californian material of Holmes (1908) from Monterrey Bay, and Barnard (1960, pls. 60, 61, part) from the Santa Barbara region, differs slightly from more northerly specimens in that the basis of peraeopod 6 (female) bulges postero-proximally more strongly.

As Barnard (1960) has intimated, the male material of *H. pennatus* (Shoemaker, 1925) from the Gulf of California appears very close to the male of *H. affinis* described here. However, even though the female has not been described, the following features of the male of *H. pennatus* would appear to justify retention of Shoemaker's form as a distinct species: Antenna 2, peduncle 5, with 5 anterior marginal calceoli; coxae 1 & 2, lower margins are setose posteriorly only, (not throughout; mandible, palp lacks proximal group of "A" setae; maxilla 1, palp 1-segmented (rather than obscurely 2-segmented); and pleon plate 3, hind process is medium-small, straight, rather than large and upcurved.

The 7.0 mm. female of "*H. oculus*" figured by Barnard (1960, pl. 60: G, I, J) from Californian Sta. 2142 also appears distinctive in the irregularly toothed hind margin of the basis of pereopod 7, and the weak hind process of pleon plate 3. In the male, peduncular segment 5 of antenna 2 is lined with 7 distinct calceoli, and the rami of uropod 3 are closely subequal and margins richly lined with plumose swimming setae. However, failing redescription of the type specimen, the information provided by Barnard (loc. cit.) is insufficient to justify its formal recognition at this time as a distinct species.

Distribution: From S. E. Alaska (near Sitka) through the Queen Charlotte Islands, north-central and south central coasts, especially in deep fiords, in bottom muds (to 600+ m. in depth), Southern Vancouver Island and San Juan Islands, south to southern California.

Heterophoxus conlanae, new species
(Fig. 31)

Heterophoxus oculus J. L. Barnard, 1960: 320-22, pls. 59-61 (part?).—Conlan 1978, lists (mainly?).—Bousfield, 1978 (in Conlan, 1978).

Material Examined:

SE ALASKA: ELB Stns. A165, Leo Anchorage, 40 m, July 23, 1961 - 2 females; ELB Stn. S13F1, Chichigof I., 0-3 m., July 31, 1980 - 2 females.

BRITISH COLUMBIA: Queen Charlotte Islands: Head of Big Inlet, C. McLean Fraser Stn. 3513, June 6, 1935 - 1 female; ELB Stn. E11, Transit I. 70 m., July 16, 1957 - 1 female ov. (7.0 mm) with slide mount, 15 other females. North-central coast: (14 station lots and 100+ specimens, as follows): ELB Stns., Calvert I. to Klawuquot Channel, July-August, 1964: H17 (1); H21 (1); H25 (24 females, 12 males, 50 im. & juvs.); H27 (1); H34 (1); H36 (1 female, 2 antepenult. males); H62 (1); H64 (1). Swanson Bay, C. Levings Stns., 51-60 m., August 18, 1975: 51B-001 (1); 51B-002 (1); 51B-003 (2 females, 1 juv.); 51B-010 (1 female ov. (5.5 mm), with slide mount); 51B-013 (1); Ibid, 51B-028, 52 m., April 4, 1976 (1).

Vancouver Island, outer coast: ELB Stn. B28, Edward King I., LW, July 10, 1976 - 3 females.

Southeastern region and Strait of Georgia: :Saanich Inlet, KE Conlan Stns., January - May, 1975: Verdier Pt. (Stn 12101), <15 m., fine sand - 1 female ov. (7.0 mm) HOLOTYPE, CMN Cat. No. NMCC1993-0041; 1 male (6.5 mm) ALLOTYPE CMN Cat. No. NMCC-0042; 45 female and 2 juvenile PARATYPES, CMN Cat. No. NMCC1993-0043.; Stn. 11132, Jan. 16 - 1 female, 2 juvs.; Stn. 12155, 10 m., Jan 15 - 4 females, 2 juveniles; Stn. 75-1-3, 8 m., Feb. 7 - 1 female; Stn. 75-1-4, Feb. 2 - 1 male penult. (6.5 mm) with slide mount, 3 females, 2 im, PARATYPES, CMN Cat.

No. NMCC1993-0044; Stn. 75-4-9, 11 m., Mar. 19 - 1 female; Stn. 1979-109, 5.1 m., May 1 - 2 females.

Saanich Inlet, K. E. Conlan Stns. (unspecified), 5 lots 7.2 - 10.8 m., Jan.-May, 1975 - 11 females, 3 males antepenult., 2 juvs., 2 im. Saturna I., JFL Hart colln., Aug. 24, 1954 - 1 male (dissected).

Sidney Region, D.V. Ellis Stns., Feb-March, 1979: Sidney Channel, Stn. 1001, 40 m., - 7 females; Stns. 1601-1602, 20 m. - 7 females; Stn. 2201, 14 m., - 7 females; Stn. 2202, 14 m. - 2 males, 2 females; Stn. 2401-2402, 24 m. - 1 female; Stn. 2602, - 1 female br. I (7.8 mm) with slide mount, 5 other females, 1 male; Stn. 3401, 16 m. - 8 females; Stn. 3502, 17 m. - 1 female.

Strait of Juan de Fuca, Victoria region, McCauley Pt., G W O'Connell collns, 26 m., Aug. 26, 1976 - 1 female ov. (6.4 mm), with slide mount, 4 other females.

WASHINGTON: San Juan Islands: Friday Harbor, at marine labs, ELB Stn. F7, night light, July 21, 1955 - 5 males; Brown Island, ELB colln., 50-60 m., Nov. 9, 1983 - 1 male; Friday Harbor, K.E. Conlan Stn. 87-14-2, 20 m., Jan. 1, 1987 - 2 females.

Diagnosis. Female ov. (7.0 mm): Rostrum nearly straight. Eye medium, subreniform, 20-25 faceted. Antenna 1, peduncle 2 with fan of 8 postero-distal setae; flagellum 9-10-segmented; accessory flagellum 6-7-segmented. Antenna 2, peduncle 4 with fan of 8-10 antero-distal strong spines; peduncle 5 long, equal to segment 4; flagellum 8-9-segmented.

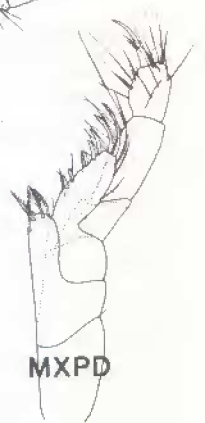
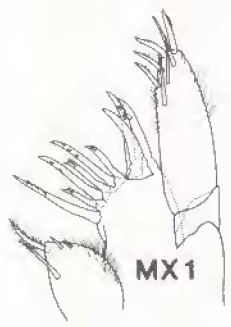
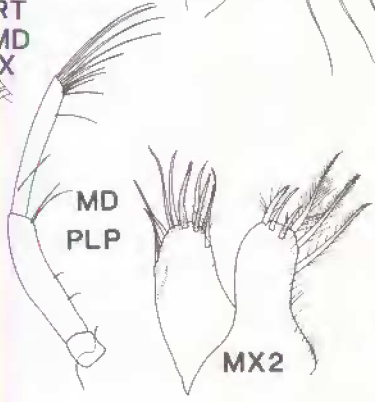
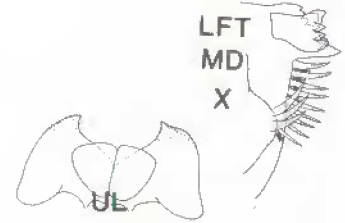
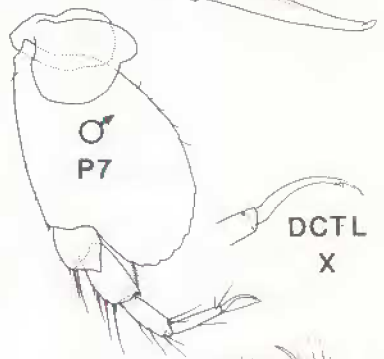
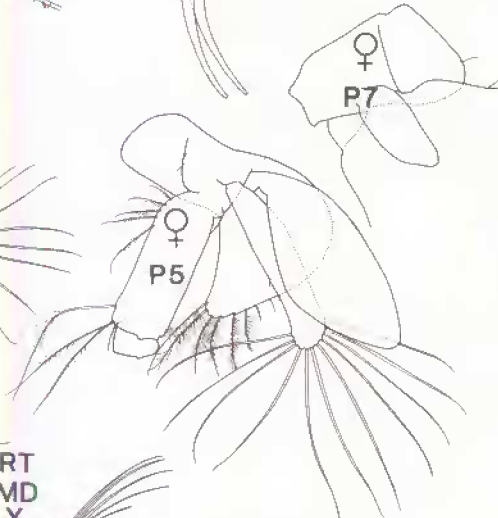
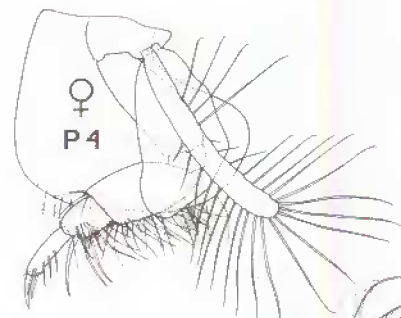
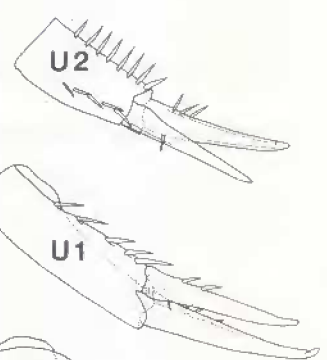
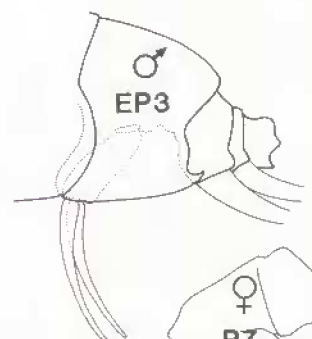
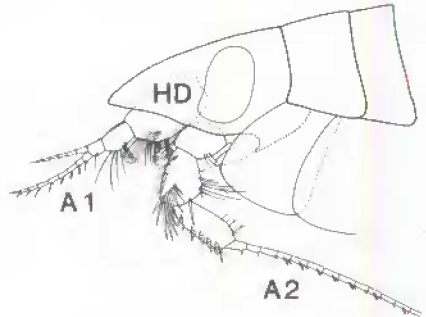
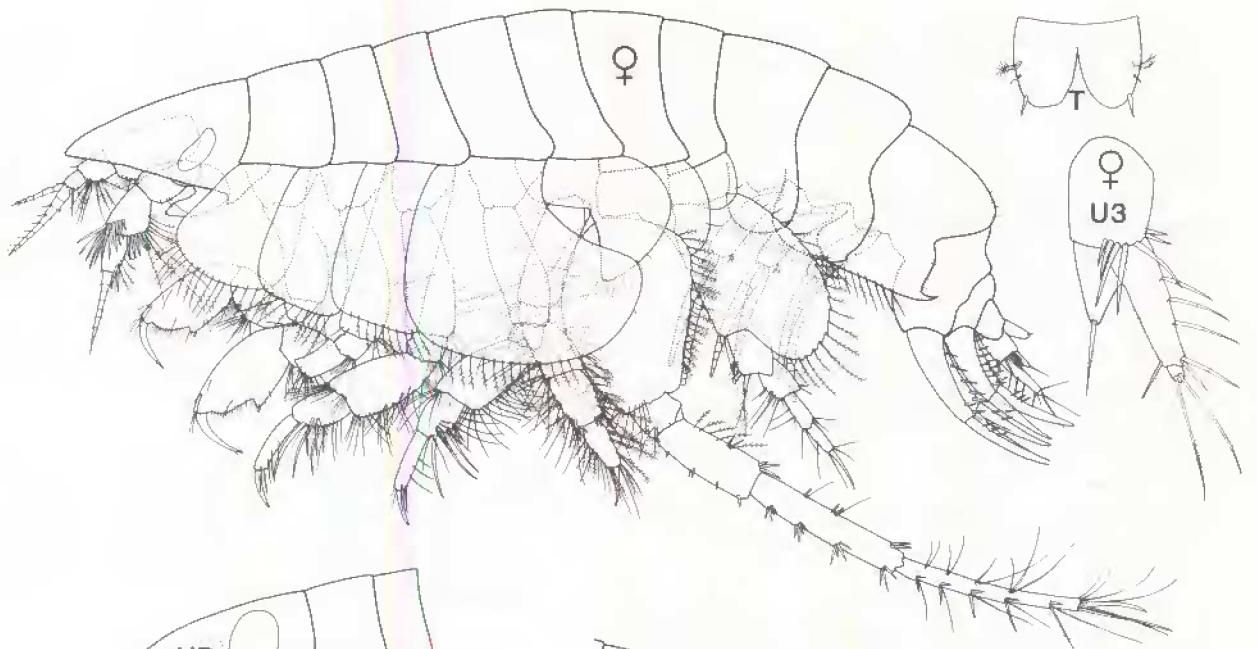
Mandible, molar short, with 3 stout apical blades; spine row with with 7-9 blades; left lacinia 8-dentate; right lacinia flabellate flabellate; palp segment 3 with single short basofacial seta. Maxilla 1 palp slender, with 4 stout apical spines. Maxilla 2 inner plate with 2-3 facial setae and 3 stout inner marginal setae. maxilliped inner plate small, narrow with 3 apical setae; outer plate with few (8-9) curved masticatory spine; palp segments 2 & 3 relatively slender.

Coxae 1-4 broad, lower margin with 18 setae; coxa 4 very large, lower margin convex. Gnathopod 2, propod distinctly larger than in gnathopod 1; carpus of gnathopod 1 with short posterior margin.

Pereopods 3 & 4, segment 5 not shortened; segment 6 with 2-3 single slender posterior marginal spines. Pereopod 5 strong, not shorter than pereopod 7; coxa, hind lobe very deep, greater than proximal margin at body. Pereopod 6, basis broad, hind margin not incised, hind setae short segment 5, hind margin with spine clusters, segment 6 with 3-5 clusters of doubly or triply grouped setae; dactyl short < 1/2 segment 6. Pereopod 7, basis not greatly expanded, hind margin with 14-16 median teeth; dactyl long > segment 6.

Pleon plate 3, hind corner very short, slightly upturned, lower margin with 7-10 setae. Pleosome 2 & 3 nearly clean,

FIG. 31 *Heterophoxus conlanae*, new species
FEMALE ov (7.0 mm) HOLOTYPE; MALE
(7.0 mm) ALLOTYPE. (SEE PAGE 131 - OPPOSITE)



lack ing dorsal "fuzz" (of *H. ellisi*). Uropods 1 & 2; ramus with 0-3 short weak marginal spines. Uropod 2, peduncle with 6-8 stout spines. Uropod 3, rami short, inner ramus about one-half length of outer ramus and shorter than peduncle.

Telson very short, lobes sub-parallel. Coxal gills lanceolate; very small on pereopod 7. Brood plates strap-like, with about 20 long apical marginal setae.

Male (7.0 mm): Eyes very large, subquadrate, nearly meeting mid-dorsally. Antenna 1, peduncular segment 2 with 6-8 strong posterior marginal plumose setae; calceoli on proximal 3-4 flagellar segments calceolate. Antenna 2, peduncle 5 longer than 4, with 7 anterior marginal calceoli; flagellum relatively short, 25-segmented, calceoli restricted to proximal 10-12 segments.

Pereopod 7, segments 5 & 6 slender, margins nearly bare, dactyl slender, strongly curved forwards.

Etymology: The species is named in honour of Dr. Kathleen E. Conlan, collector of the type material, who has contributed extensively on the systematics of N. American Pacific corophioideans and on reproductive behaviour in amphipod crustaceans generally.

Taxonomic Commentary: *Heterophoxus conlanae* is similar to the austral species, *H. videns* K. H. Barnard, having setose posterior margins on segments 5 & 6 of pereopod 6, but is much smaller, among other differences.

Distribution: The species ranges from southeastern Alaska (Sitka region), widely through British Columbia, to Washington State, in silty sands from the tide lines to about 40 m.

Heterophoxus ellisi, new species
(Fig. 32)

Heterophoxus oculatus: Bousfield (in Conlan, 1978) (part)?
—Austin, 1985: 598(part)?—Staude, 1987: 380+key (part)?

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands: Big Inlet, C. McLean Fraser Sta. 3513, June 6, 1935 - 1 female br. 11 (8.0 mm), 4 other females, 1 male (6.0 mm), with slide mount.

Southeastern mainland coast. Burrard Inlet: ELB Stn. P2, 20 m. mud, Nov. 2, 1977 - 1 female.

Southern Vancouver Island: Berkeley Sound region: ELB Stns. B14, May 25, 1977 - 1 female; B14, Trevor Channel, 44-54 m., mud - 1 female; Stn P26, Koprino Harbour, May 25, 1975 - 12 specimens. Inner coast: French Creek, near Nanaimo, P. O'Rourke Stn. FC8, Aug. 23, 1977 - 1 female. Sidney region, D. V. Ellis collections: N.W. James Spit, 16.5 m. sandy silt, Mar. 8, 1979 - 1 female ov. (6.8 mm) with slide mount, 1 female (6.8 mm) HOLOTYPE, CMN Cat. No.

NMCC1993-0045; 1 female PARATYPE, CMN Cat. No. NMCC1993-0046; Miner's Channel, Stn 3502, 17 m., sandy silt, March 9, 1979 - 1 male (7.0 mm) ALLOTYPE, CMN Cat. No. NMCC1993-0047; 1 female PARATYPE, CMN Cat. No. NMCC19923-0048. Sidney Channel, Stn. 1001, 40 m., Feb. 9, 1979 - 3 females; Haro Strait, Stn. 2201, 14 m, Feb. 23, 1979 - 1 male (antepenult); Boatswain Bank, Stns. 1601-1602, 20 m., Feb 15, 1979 - 1 female.

Saanich Inlet, K.E. Conlan colln, May 1, 1975 - 1 female. Victoria region: McCauley Point, G. W. O'Connell coll., 49 m., silty sand, Aug. 26, 1976 - 2 males.

Vancouver I., outer coast: ROM Tully Cruise, Stn. 11A, 1988-030 - 1 female.

WASHINGTON: Friday Harbor, San Juan Islands, ELB Sta. F7, night light, July 21, 1955 - 2 males; *ibid.*, KEC Stn. 87-14-2, 20 m., Jan. 1, 1987 - 7 females, 4 males. ELB Sta. W39, Neah Bay, LW level, July 30, 1966 - male (6.2 mm) with slide mount, 2 other males.

Diagnosis. Female (6.8 mm): Rostrum large, slightly downcurved distally. Eye small, sub-reniform, close to lower head margin. Antenna 1 peduncular segment 2 with posterodistal fan of 7-8 plumose setae; flagellum with 8-9 segments, accessory flagellum with 5-6 segments. Antenna 2, peduncle 4 short, with 7-8 very long posterior marginal setae and antero-distal fan of 9-10 strong spines; flagellum 8-segmented.

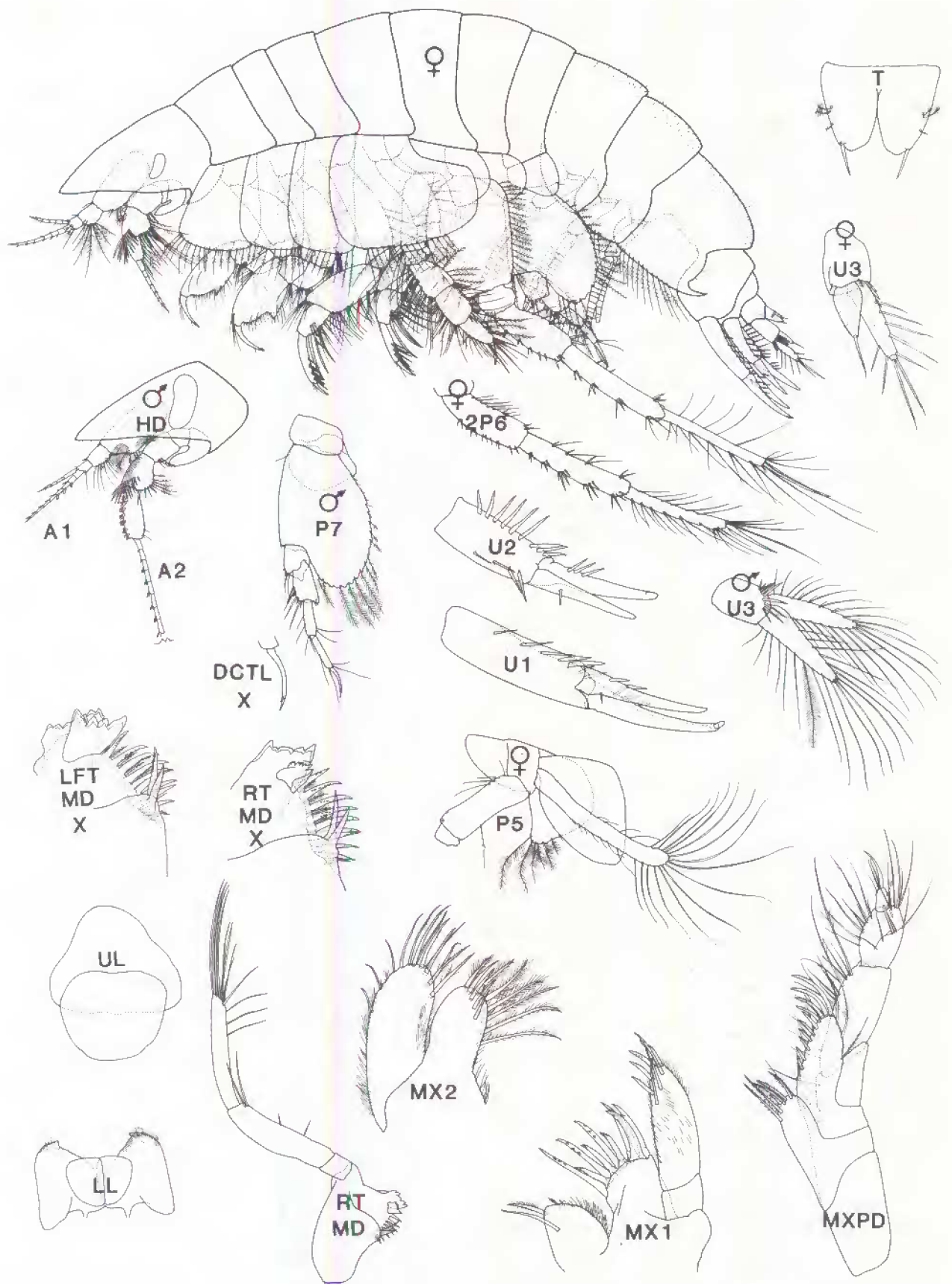
Mandible, molar with 2 stout apical blades; spine row with 8-9 blades, left lacinia 7-8 dentate, right lacinia flabellate; palp segment 3 lacking baso-facial setae. Maxilla 1, palp slender apex acute. Maxilla 2, inner plate with 4-5 facial setae, and 4-6 stout inner marginal setae. Maxilliped, inner plate medium, with 4-5 long apical setae; outer plate with ~10 curved masticatory spines; palp segments 2 & 3 medium.

Coxae 1-4 broad, relatively shallow, lower margins with ~21 setae. Coxa 4, length 1.5 times depth. Gnathopod 1, carpus short; propod smaller than in gnathopod 2.

Pereopods 3 & 4, segment 5 not broadened, segment 6 slender, inner distal margin with 4-5 groups of medium spines; dactyls short < 1.2 segment 6. Pereopod 5 strong, not shorter than pereopod 7; posterior coxal lobe medium, about as deep as width at body attachment; segments 4 & 5 distinctly broader than segment 6. Pereopod 6, basis broad, hind margin straight, setose; segment 5 with a fewer posterior marginal spines, segment 6, hind margin with 5-6 singly inserted long setae, anterior margin with pairs of long spines and setae; dactyl long > 1/2 segment 6. Pereopod 7, basis with 14-18 weak posterior marginal teeth; dactyl slender length > segment 6.

Pleon plate 3, tooth at hind corner slender, nearly straight, lower margin straight with about 12 setae. Uropods 1 & 2,

FIG. 32. *Heterophoxus ellisi*, new species
FEMALE ov (6.8 mm) HOLOTYPE; MALE ALLOTYPE (7.0 mm) (SEE PAGE 133 - OPPOSITE)



rami each proximally with 1-3 short spines. Uropod 2, peduncle with 8-9 tall outer marginal spines. Uropod 3, rami short, inner ramus about equal in length to peduncle.

Telson lobes medium, converging distally, apical spines relatively long.

Male (7.0 mm): Eyes large, medium reniform. Antenna 1, proximal 3 segments of flagellum calceolate. Antenna 2, peduncular segment 5 longer than 4, with 7 anterior marginal calceoli; flagellum elongate (30+ segments) with at least 6 proximal adjacent segments. Peraeopod 7, segments 5 & 6 very slender, dactyl slender, curved forward, shorter than segment 6. Uropod 3, rami subequal, margins relatively richly plumose-setose.

Etymology: The species is named in honour of Dr. Derek V. Ellis, Professor of Biology, University of Victoria, collector of the TYPE material, and a significant contributor to knowledge of the taxonomy and ecology of benthic marine invertebrates of the Canadian Pacific region.

Distribution: Occuring in the region of southern British Columbia to the San Juan Islands and Strait of Juan de Fuca, in fine sands at medium depth (an isolated early record from the Queen Charlotte Islands requires more recent confirmation).

Taxonomic Remarks: This species shows affinities with *Heterophoxus conlanae*, but entrains a mixture character states that are generally more pleiomorphic. A more apomorphic variety is described below.

Heterophoxus ellisi, variant
(Fig. 32.2)

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands region: Dixon Entrance, J. W. Scoggan Stns. 105, West of Celestial Reef (54° 27' N, 131° 42' W), sand, mud, 155 m., August 12, 1965 - 25 females, incl. 1 female br. II (9.0 mm), with slide mount. Hecate Strait, JWS (FRB) Sta. 104 5-65-83, Aug. 11/65 - 2 females.

North-central coast: Ocean Falls, C. Levings Stns. 24B-013, July 19, 1972 - 1 female im.; Stn. O5, Dec. 3, 1972 - 1 male; Sta. 51B045, Aug. 18, 1974 - 1 male, with slide mount; Stn. 51B047, Aug. 18, 1974 - 1 female.

Vancouver Island: Queen Charlotte Sound, N.A. Powell coll., 190 m., Aug. 14, 1967 - 2 males, antepenult. Off outer coast, IOC Stn. DS405-1, 1979-81 - 1 female.

Diagnosis. Female (7.0 mm): Differing from typical *H. ellisi* by the presence of spines and setae on the posterior margin of segment 5 of P6, and by special spines on outer ramus of uropod 2 in the male. The taxonomic significance of these spines could not be fully ascertained because of the limited number of males in this material.

Distribution: Known only from the north and central coasts and northern Vancouver Island, British Columbia, on fine sand bottoms, in depths to 155 m.

Extralimital Species. Several other morphotypes of *Heterophoxus* have been recorded from coastal waters from southern California to Baja California. Some have been formally named, and others were described or figured as variants under the names *Heterophoxus oculatus* and/or *H. affinis*. Although these records are outside the immediate geographical scope of this study, because the genus is apparently endemic to the North American Pacific coastal marine region, we make the following brief comments on these forms, and have included them in the key, to the limit of their determinable distinctive character states.

(1) *Heterophoxus oculatus* (Holmes). This species was described reasonably accurately and his figures are included here for comparative purposes (Fig. 29B). His species seems closest to *H. conlanae*, and *H. ellisi* newly described in this text. In the double clusters of setae on the hind margin of segment 6 and in the rounded hind margin of the basis of peraeopod 6, it appears closer to *H. conlanae*. It differs from the latter, however, in the stronger setation of the lower margin of coxa 1, and pleon plate 3, the stronger distal segments of the maxilliped palp and the relatively longer and more strongly setose inner ramus of uropod 3. Barnard (1960, *loc. cit.*) partial figures of a mature male of "*H. oculatus*" from Friday Harbor, Puget Sound appear close to our illustrations of *H. conlanae*. To date, material identical with the *H. oculatus* of Holmes (1908) has not been found in northern collections.

(2) *Heterophoxus* sp. 1. The 7.0 mm female of "*H. oculatus*" figured by Barnard (1960, pl 59) from California Stn. 2448 is similar to *H. affinis* in having a strongly produced Ep3, and nearly lacking hind marginal setae on segment 6 of peraeopod 6. However, it is distinctive in the very broad form of coxa 4, the relatively elongate segments 4-6 of peraeopod 5, and the presence of spines and setal groups on the posterior margin of segment 5 of peraeopod 6, among other features. It is recognized herein as *Heterophoxus* species 1 (p. 126, key).

(3) *Heterophoxus oculatus nitellus* Barnard, 1960, p. 320, -1. 61 A-F. We agree with the distinctive features of this taxon illustrated by Barnard (*loc. cit.*) but would elevate it to full species status as *Heterophoxus nitellus* Barnard.,

(4) *Heterophoxus pennantus* Shoemaker, 1925:25, figs. 1-3. The description was based on a 5 mm male taken at a marine night light in the Gulf of California. Its overall morphology is clearly referable to the *affinis* type of Holmes (1908) but differs in the following character states: coxa plates 1-3 with few (<10) lower marginal setae; coxa 5, peraeopod 5, hind lobe deep; mandibular palp segment 3 lacking basofacial setae; and gnathopod 1, carpus with short posterior margin. In view of these differences, and also of the small size of the mature animal and its isolated geographical location, we prefer to retain this taxon as a valid full species.

Harpiniopsis Stephensen

Harpiniopsis Stephensen, 1925: 171.—J. L. Barnard, 1958: —J. L. Barnard, 1960: 325.—Barnard & Karaman, 1991: 612.

Harpinia: Gurjanova, 1951: 365 (partim).

Type species. *Harpiniopsis similis* Stephensen, 1925, monotypy.

Species N. Pacific general region: *Harpiniopsis amundseni* Gurjanova, 1946 [227]. (Arctic-eastern Siberia); **H. fulgens* Barnard, 1960 [332] pls. 67, 68. (California to B. C.); **H. gurjanovae* (Bulycheva, 1936) [251]. (Bering Sea to B. C.); **H. kobjakovae* (Bulycheva, 1936) [254]. (Japan Sea to Bering Sea); *H. miharaensis* (Nagata, 1960) [395]; *H. moiseevi* (Gurjanova, 1953) [286]; *H. orientalis* Bulycheva, 1936 [391] (Japan Sea.); **H. pacifica* (Bulycheva, 1936) [252]. (Japan Sea); *H. percellaris* Barnard, 1971 [66] fig. 42; **H. salebrosa* (Gurjanova, 1936) [248]. (Chukchi & Bering Seas, med. d.); **H. schurini* (Bulycheva, 1936) [250]. (Japan Sea to Bering Sea); **H. tarasovi* (Bulycheva, 1936) [248] (Japan Sea, Bering Sea); **H. triplex* Barnard, 1971 [310A] fig. 43.

Diagnosis: Pigmented eyes lacking. Rostrum large, unstricted laterally, often mid-dorsally ridged. Antenna 1, peduncular segment 2, posterior setae confined apically; basal flagellar segment(s) (in male) forming a weak callynophore (with group of enlarged aesthetascs). Antenna 2, segment 1 not (or weakly) ensiform; peduncular segment 3 with fan of 3 (or more) posterior marginal setae; segment 5 distinctly narrower than segment 4; in males, segments 3 & 4 with anterior marginal brush setae; segment 5 normally with 2 antero-distal calceoli; flagellum elongate, proximal segments (in some species?) with vestigial calceoli.

Lower lip, outer lobes with distal cones. Mandibular palpal hump of medium size; molar of type 6 (2-3 apical blade spines); left lacinia 4-dentate, right lacinia simple, bifid, or flabellate, with multiple teeth(?); right incisor with 3-6 teeth. Maxilla 1, outer plate with 7-11 slender apical spines; inner plate with 2-3 apical plumose setae. Maxilla 2, plates subequal, facial setae of inner plate subapical. Maxilliped, outer plate short, spines medium, pectinate; palp slender, segment 3 not distally produced; dactyl usually reduced, but with distinct elongate unguis.

Coxae 1-4 wide, deep. Gnathopods 1 & 2, propods small, similar, palms oblique; carpus short, shallow, weakly setose free hind margin.

Peraeopods 3 & 4, segment 6 slender, not spatulate. Peraeopod 5, segment 2 narrow; coxa, hind lobe deep, subacute. Peraeopod 6 basis broad, distal segments

slender, weakly armed. Peraeopod 7, segment 5 apparently unmodified, but dactyl longer, curved, in male.

Pleon plate 3, hind corner usually produced as an up-turned tooth. Uropod 1, peduncle lacking apical displaced spine. Uropod 3 aequiramous, rami bare, terminal segment of outer ramus large.

Telson lobes medium to long, fused basally 1/8 to 1/2.

Distributional Ecology: The genus is well represented in the North Pacific region especially in deeper softer sediments of the outer shelf. Three species are not uncommon in coastal sediments from the Bering Sea to Central California, but relatively rare south of Pt. Conception.

Taxonomic Commentary: The generic status of *Harpiniopsis* was reconfirmed by Barnard (1958) mainly on the basis of the very elongate flagellum of antenna 2 in the male; this character separates it from the genus *Harpinia* whose members are more specialized, and occur mainly in the North Atlantic region. Although males of most of the N. Pacific species of Harpiniinae are unknown, those studied here (and in lit.) conform with Barnard's distinctive male antennal character state (above). Thus, species for which females only are known are also assigned (tentatively) to *Harpiniopsis*. However, the diversity of mouthpart structure (in mandibular palp, maxilla 1 and maxilliped armature, etc.) exhibited by component species may provide bases for subgeneric, if not full generic subdivision, within the species complex.

A key to world species of the genus was provided by Barnard (1960, *loc. cit.*) with further detailed commentary on regional species (e.g. *H. triplex*) by Barnard (1971). Regretably, this deeper water genus was represented by very few species in present study material, and so the authors are able to add little to previous information or usefulness of previous keys. Species likely to be obtained in deep offshore waters of British Columbia would include the following taxa:

- (1) *H. gurjanovae* Bulycheva, 1936 (Bering Sea to B. C.)
- (2) *H. percellaris* Barnard 1971 (off Oregon)
- (3) *H. triplex* Barnard, 1971 (Oregon, v. deep)
- (4) *H. salebrosa* (Gurjanova, 1936) (Japan, Bering Sea)
- (6) *H. kobjakovae* (Bulycheva, 1936) (Bering Sea)
- (7) *H. schurini* Bulycheva, 1936 (Japan, Bering Seas)
- (8) *H. tarasovae* Bulycheva, 1936 (Japan, Bering Seas)
- (9) *H. galera* Barnard, 1960 (C. Calif, shallow)
- (10) *H. fulgens* Barnard, 1960. (British Columbia to C. California?)

Harpiniopsis fulgens J. L. Barnard
(Fig. 33)

Harpinia fulgens Barnard, 1960: 310, plate 67.

Material Examined: More than 260 specimens (in 180 lots) of which 140 were mature females, 55 juveniles or immatures, 7 penultimate males, 9 mature males, and 50 dried indeterminates (mostly subadult females), all in collections of the CMN, as follows:

BRITISH COLUMBIA: North-Central coast: Ocean Falls, 1974, C. Levings Stns. 51B-142,-047 - 10 females; 1977 C. Levings Stn. 28B-18 - 1 female.

Southeastern coast: Jervis Inlet, 1977, ELB Stn. J1- 2 females; Queen Charlotte Channel, 1977, ELB Stns.: P7, off Bowen Island 1 female ov (3.5 mm), with slide mount (fig'd), CMN Cat. No. NMCC1992-1111; ELB Stn. P8, off Passage I. - 1 male (3.5 mm), with slide mount (fig'd), CMN Cat. No. NMCC1992-1110. Burrard Inlet, C. Levings Stn. B9, 1977 - 1 female; Jervis Inlet, ELB Stns. P1, P2, 300-400 m., Nov. 2, 1977 - 11 females; Indian Arm, ELB Stn. E5, 60 m. mud & coarse sand, Nov. 4, 1977. - 10 females.

South Vancouver Island: French Creek, P.O'Rourke Stn. FC3, August, 1977 - 1 female.

Vancouver Island, outer shelf, Institute of Ocean Sciences Patricia Bay, B. C.: 1979 (May, July, August,) Queen Charlotte Islands, 100-300 m. 10+ females. NMNS Access. No. 1983-57. Additional IOS lots taken off Vancouver Island during June-August, and the following year, from April - August, 1981, contained numerous lots of material tentatively identified as this species, but not examined in detail.

Diagnosis. Female ov. (3.5 mm): Rostrum with weak mid-dorsal keel, apex slightly downturned. Inferior lateral head lobe strongly produced, upturned. Antenna 1, flagellum 6-segmented; accessory flagellum 5-segmented.

Mandible, molar with 2 large apical blades; spine row with 5-6 blades, left lacinia 6-7 dentate; right lacinia flabellate; palp segment 3 with proximal facial cluster of 3 long "A" setae and a few posterior marginal "C" setae. Maxilla 1, outer plate with 11 apical spines; inner plate with 2 apical setae; palp weakly 2-segmented, apex with 5-6 slender spines. Maxilla 2, inner plate with 2 sub-apical facial setae. Maxilliped, inner plate apically with single spine and 4-5 plumose setae; outer plate slender, straight, with 8-9 marginal pectinate spines; unguis of dactyl elongate (2 X body).

Gnathopods, propods closely subsimilar; carpus of both short, hind lobe narrow.

Peracopods 3 & 4, segment 5 short, nearly as deep as long; segment 6, hind margin distally long-spinose, dactyls medium. Peracopod 5, coxal hind lobe distinctly shorter than basis; segments 5 & 6 elongate, subequal. Peracopod 6, basis, anterior margin expanded medially, hind margin

straight; distal segments elongate (segment 6 longer than basis), very weakly spinose. Peracopod 7, basis, postero-distal margin rounded, with numerous shallow serrations; segment 4-6 with anterior pairs of slender spines; dactyl very slender, longer than segment 6.

Pleon plate 3, hind process short, straight, not upturned; lower margin proximally with about 6 slender spines. Uropods 1 & 2, peduncles with several slender outer marginal spines; both rami with 2-3 slender posterior marginal spines. Uropod 3, rami smooth, outer slightly longer, terminal segment elongate (> 1/2 proximal segment).

Telson lobes medium, fused 1/5 basally, apices subacute, each with 2 disto-lateral slender spines; paired penicillate setae long,, disto-laterally inserted.

Coxal gills irregularly sac-like, medium broad, subacute distally, small on peracopod 7. Brood plates regular.

Male (3.5 mm.): Antenna 1, flagellar segment 1 with 3-4 aesthetascs (weakly callynophorate), but no calceoli. Antennae 2, segment 4 strongly expanding antero-distally, with strong antero-distal fan of 8-10 slender spines; segment 5 slightly broadened behind, with 2 antero-distal calceoli; flagellum with 30-35 segments; segments 1, 3, 5 & 7 with minute vestigial calceoli. Peracopod 7, distal segments and dactyl only slightly less robust than in female.

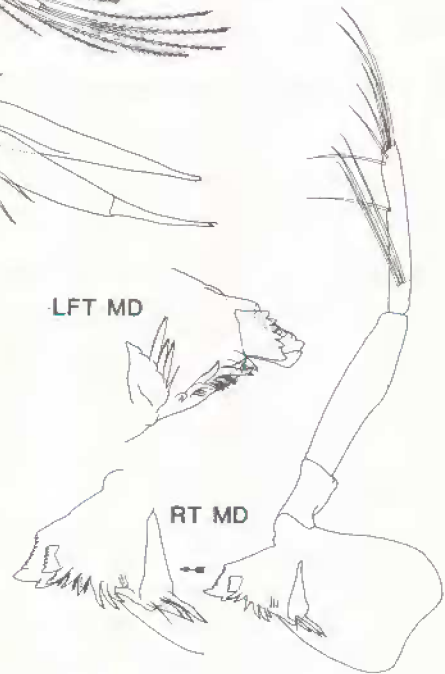
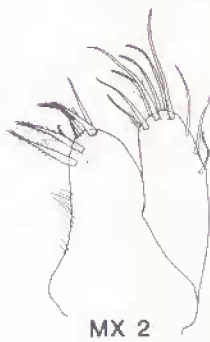
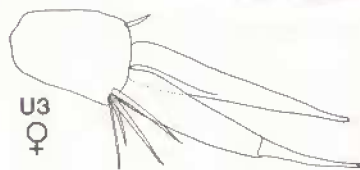
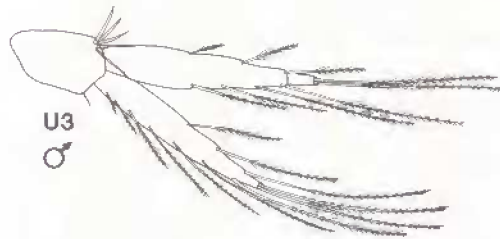
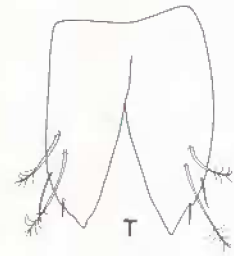
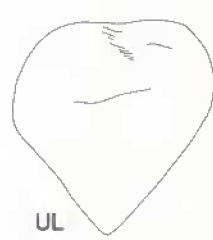
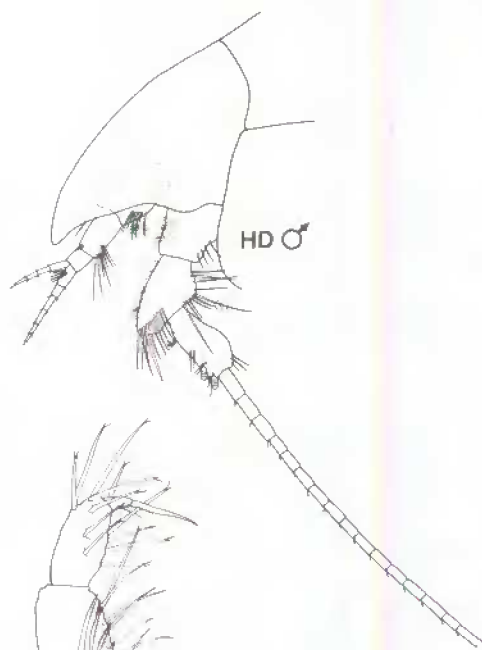
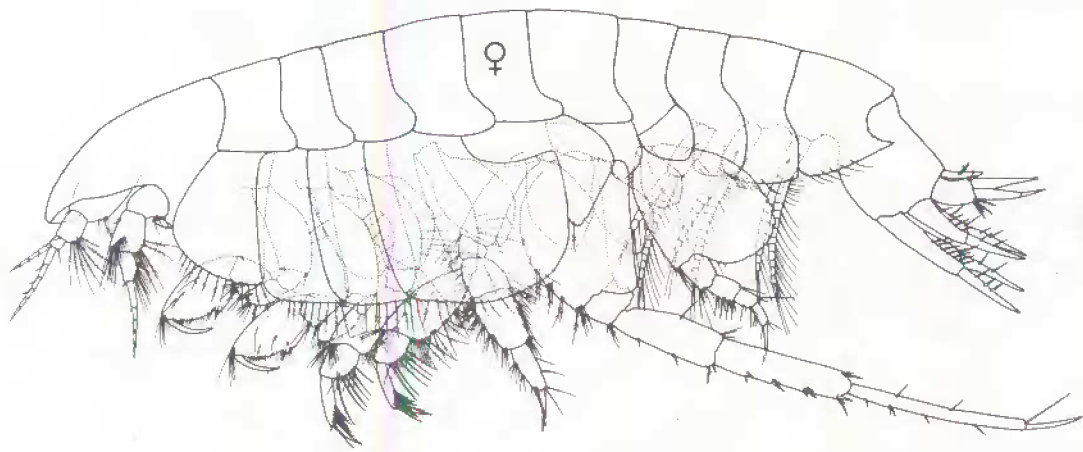
Uropod 3, rami slender, subequal, marginals with 3-6 plumose setae, outer ramus lacking distinct terminal segment.

Taxonomic commentary: Northern material is closely similar to that illustrated by Barnard (1960, pls. 67-68) except for minor differences in the shape of coxa 1, basis of peracopod 6, form of the hind tooth on pleon 3, and spination of uropod 1. It is separable from *H. gurjanovae* by the very obvious difference in shape of the hind margin of the basis of peracopod 7, by the very much longer distal segments of peracopod 6, and by the presence of baso-facial setae on mandibular palp segment 3.

As noted below, this species is remarkably unlike *H. gurjanovae* diagnosed below. In many respects, especially the form of the mandibular palp, and uropod 3, it appears closer to species of the genus *Pseudharpinia*. A major revision of this deep-water genus is urgently needed.

Distributional Commentary: The species ranges from California north to British Columbia (but has not yet been taken in southeastern Alaska) in depths of 100-500+ metres, and to more than 2000 m. in the San Clemente Basin, California.

FIG. 33. *Harpiniopsis fulgens* J. L. Barnard.
FEMALE ov. (3.5 mm); MALE (3.5 mm)
(SEE PAGE 137 - OPPOSITE)



Harpiniopsis gurjanovae Bulycheva
(Fig. 34)

Harpiniopsis gurjanovae Bulycheva, 1936: 251, figs. 20-23 H.—Gurjanova, 1951: 368, fig. 217.

Material Examined: P. Slattery collns, Bering Sea region, 1980-1982, June-October, 8 lots, in depths of 20-25 m.: St. Lawrence I., July 10, 1980, 2 lots including 1 female ov. (3.5 mm), + slide mount, HOLOTYPE, CMN Cat. No. NMCC1992-1112. Additional lot from Unimak I. (no other data) - 1 specimen.

Diagnosis. Female ov. (3.5 mm): Inferior lateral head lobe short, straight, not upturned, acute. Antenna 1, peduncular segment 2 with fan of 5-6 postero-distal plumose setae; flagellum 5-segmented; accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 little expanded, with 5-8 posterior marginal plumose setae and antero-distal fan of 9-10 slender spines; segment 5 shorter than 4; flagellum with 5 longish segments.

Mandible, molar with 3 stout apical blades; spine row short, with 4-5 large pectinate blades; left lacinia 4-5 dentate, right lacinia flabellate; palp elongate, segment 3 longer than segment 3, lacking "A" and "C" setae. Maxilla 1, outer plate with 7 apical spines, inner plate with 3 short apical setae; palp clavate, rounded apex with 3-4 slender spines. Maxilliped, inner plate broad, with 3 strong plumose spines; outer plate very short, not exceeding palp segment 1, inner margin with 5-6 pectinate marginal spines; palp segment 3 large, dactyl normal, unguis and body subequal in length.

Coxae 1-4 relatively narrow, coxa 1 not broadened distally, lower margins with few (<10) plumose setae. Coxa 4 enormous, broad and deep. Gnathopods subsimilar, but carpus of gnathopod 1 with distinct posterior border.

Peraeopods 3 & 4, segment 5 distinctly longer than deep; segment 6 spinose posteriorly only near apex; dactyl very long about equal to segment 6. Peraeopod 5, coxal hind lobe very deep, as long as basis; segments 5-6 short, 5 nearly as wide as long. Peraeopod 6 relatively short; basis expanded antero-distally, hind margin nearly straight; distal segments not elongate (atypical in this specimen? - segment 6 shorter than basis); dactyl nearly equal in length of segment 6. Peraeopod 7, basis, posterior margin irregular, postero-distally with two large acute teeth separated by a blunt tooth, and a fourth acute distal tooth; segments 4-6 with singly inserted anterior slender spines; dactyl very long, longer than segment 5 & 6 combined.

Pleon plate 3, hind corner with short, upturned tooth; lower margin distally with 4 short setae. Uropods 1 & 2, peduncles sparsely spinose; inner ramus smooth, outer medially with closely set paired posterior marginal spines. Uropod 3, rami medium, longer than peduncle, nearly bare, outer ramus slightly the longer, terminal segment short (<1/2 proximal segment).

Telson lobes relatively narrow, elongate, fused basally,

apices bluntly rounded, with subapical outer marginal seta; penicillate setae, short, inserted proximally.

Male: Unknown.

Taxonomic commentary: This species contrasts strongly, in several major character states, with *Harpiniopsis fulgens*. These differences include the number of apical teeth on the outer plate of maxilla 1, the much reduced maxilliped outer plate, the very different structure of the mandibular molar and lacinia, as well as obvious differences in the form of the basis of peraeopod 7. In any other taxonomic group, these differences would be considered to be of generic value. A major revision of this genus on a world basis appears urgently needed.

Distributional Commentary: ?The species is recorded from the Bering Sea and Sea of Okhotsk but is unknown further south on the North American coast.

Pseudharpinia Schellenberg

Pseudharpinia Schellenberg, 1931: 81.—J. L. Barnard, 1960: 342.—Barnard & Drummond, 1978: 533.—Barnard & Karaman, 1991: 628.

Type species. *Pseudharpinia dentata* Schellenberg 1931, monotypy.

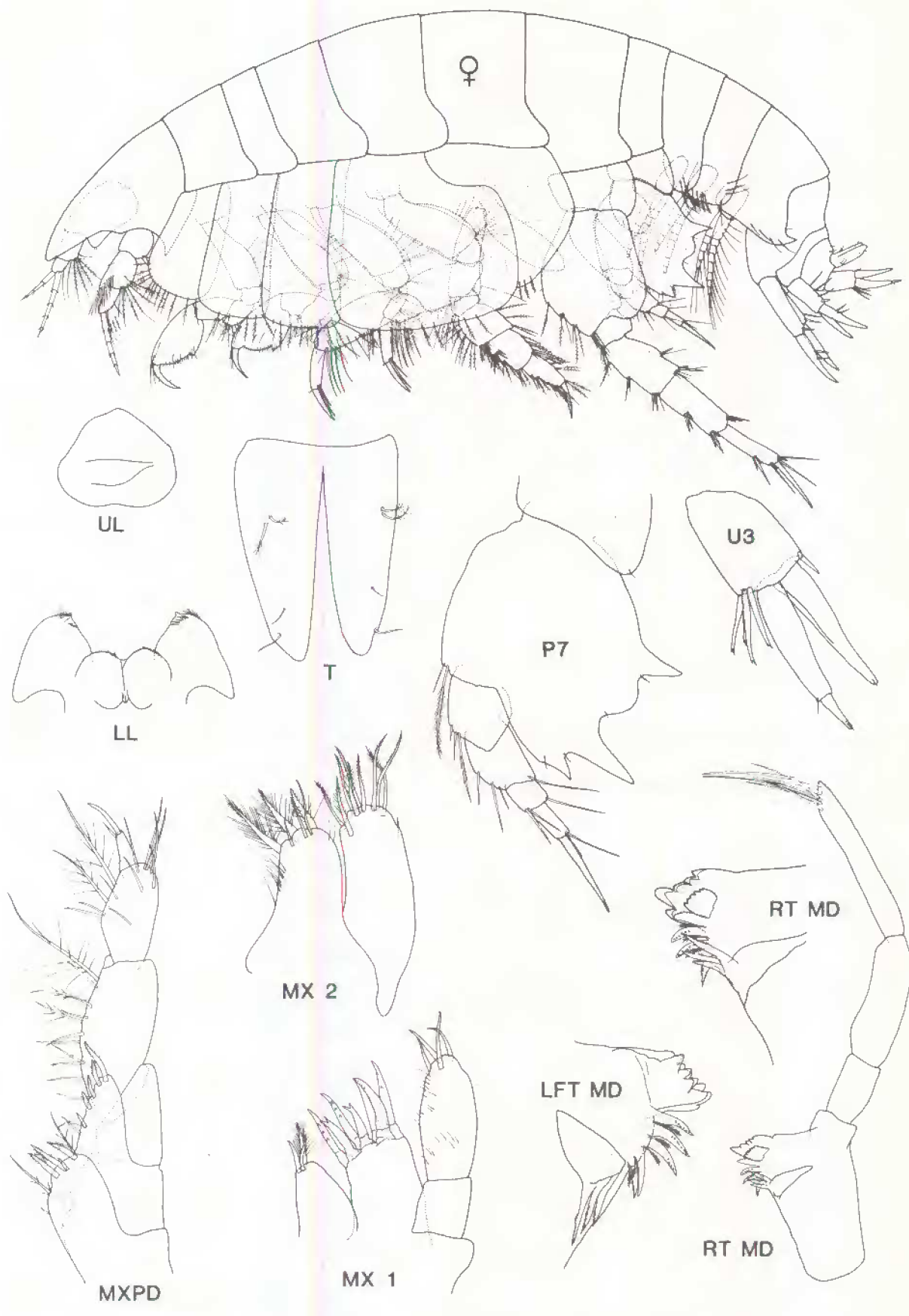
Species (North American Pacific region): *Pseudharpinia sanpedroensis* Barnard, 1960 [329]; 1967 [423AB]; *P. cinca* Barnard, 1961 [735]; *P. productus* Barnard, 1964 [501A] (as *P. abyssalis productus*); *P. inexpectata*, new species. non *Pseudharpinia excavata* (Chevreux, 1887).

Diagnosis: (see Barnard & Karaman, *loc. cit.*). Rostrum full, nearly straight, inferior head lobe acute. Pigmented eyes lacking. Antennae short. Antenna 1, peduncle 2 very short. Antenna 2, segment 1 strongly ensiform; in male, peduncular segment 5 calceolate; flagellum elongate, possibly weakly calceolate.

Mouthparts: mandibular molar small, apex with 2-4 blades; raker blades short, thick; palp slender, weakly setose. Maxilla 1, outer plate with 9 apical spines; palp 1 or 2-segmented. Maxilliped reduced; palp, dactyl small, with long apical spine.

Coxae 1-4 very broad, 1 expanded distally, lower margins with spaced plumose setae. Coxa 4, lobe rounded behind. Gnathopods 1 & 2 relatively strong, propods obliquely subchelate, subsimilar, carpus of both short. Peraeopod 5 strong, coxal hind lobe deep, dactyl short. Peraeopod 6, distal segments with anterior slender spines (as

FIG. 34. *Harpiniopsis gurjanovae* Bulycheva
FEMALE ov. (3.5 mm).
(SEE PAGE 139 - OPPOSITE).



in *Heterophoxus*). Peraeopod 7, basis with strong antero-distal plumose setae.

Pleon plate 3, hind corner with strong tooth or process. Uropods 1 & 2 ordinary, rami strongly spinose marginally. Uropod 3, rami short, unequal, outer ramus marginally terminal segment short, weakly setose.

Telson lobes short, fused basally, rounded apically. Coxal gills large on peraeopods 2-6, very small on peraeopod 7.

Male: Mature male unknown. Antenna 2 probably elongate.

Taxonomic Commentary. This genus embraces nearly as much morphological diversity as does *Harpiniopsis*, and similarly is in need of extensive revision. It is clear that *P. excavata* (Chevreux, 1887) described originally from the North Atlantic region, is very distinct from Barnard's *sanpedroensis* from the coast of California, and even more distinct from the present material from the coast of British Columbia.

Distributional Commentary. The 12 world-wide species of this genus occur mainly in soft sediments of the cold, deep shelf waters to abyssal depths.

Pseudharpinia inexpectata, new species
(Fig. 35)

Pseudharpinia sanpedroensis Barnard, 1960: 329, plates 64, 65 (part).

Pseudharpinia excavata Barnard, 1966 (Bull. Amer. Mus. Nat. Hist. 127).

Material Examined:

BRITISH COLUMBIA: Southeastern coast, Burrard Inlet, C. Levings Stn., Sept. 1, 1977 - 1 female br II (4.5 mm) + slide mount, HOLOTYPE CMN Cat. No. NMCC1993-0092.

Off Vancouver Island (IOS Stns. several samples). Stn 2 A1-BM, 1979-81 - 1 female subadult (3.5 mm), + slide mount (fig'd), PARATYPE, CMN Cat. No. NMCC1993-0073.

Diagnosis. Female (4.5 mm): Rostrum slender, slightly downcurved at acute apex; lower margin long, smoothly arcuate. Inferior head lobe short, acute. Antenna 1, peduncular segment 2 small, with postero-distal cluster of 4-5 plumose setae; flagellum 5-segmented, accessory flagellum 3-segmented. Antenna 2, peduncular segment 4 distally broadening, hind margin with fan of 6-8 plumose setae, antero-distally with distally with fan of 8-10 slender spines; flagellum 5-7-segmented.

Mandible, molar, apex with 2 stout and 2 weak blades; spine row short, with 4-5 heavy pectinate blades; left lacinia

4-dentate, right lacinia flabellate; incisor 4-dentate; palp segment 3 long, slender, subequal to segment 2, lacking cluster of A-setae or posterior marginal "C" setae. Maxilla 1, inner plate with 2 short subapical setae, outer plate with 9 apical pectinate spines; palp 2-segmented, apex with 3 stout setae. Maxilla 2, inner plate with single sub-apical facial seta; inner margin with 2 stout plumose setae. Maxilliped, inner plate "thumb-like" apex with a few slender setae; outer plate short, with 5 very unequal, curved, masticatory spines; palp segment 2 columnar; dactyl with short body and slender unguis.

Coxa 1 strongly broadening distally, lower margin with 8-9 plumose setae. Coxa 4, hind lobe very broadly rounded. Gnathopod propods closely subsimilar, propod palmar margins oblique; basis lacking posterior marginal setae.

Peraeopods 3 & 4, segment 5 stout, with single slender postero-distal spine; segment 6 slender arched, posterior margin spine cluster distally only; dactyls medium > 1/2 length of segment 6. Peraeopod 5, coxal hind lobe deep, anterior margin nearly perpendicular; basis short, little longer than segment 5, dactyl short, < 1/2 segment 6. Peraeopod 6, segments 5 & 6 not elongate, not exceeding length of basis, dactyl not > 1/2 segment 6. Peraeopod 7, basis with weak antero-distal setal cluster, hind lobe not broadly expanded, hind margin irregularly serrate; dactyl normal, not longer than segment 6.

Pleon plate 3 hind process strongly produced, sickle-shaped, lower margin long, slightly emarginate, lined with 6-8 setae. Uropods 1 & 2, inner ramus bare, outer ramus with middle spines. Uropod 3, outer ramus slender, distinctly exceeding inner, terminal segment minute inner ramus about equal in length to peduncle having a strong inner distal fan of 5 stout spines.

Telson lobes fused basally, slightly diverging distally, apices rounded, each with slender sub-apical spine, sand median penicillate setae.

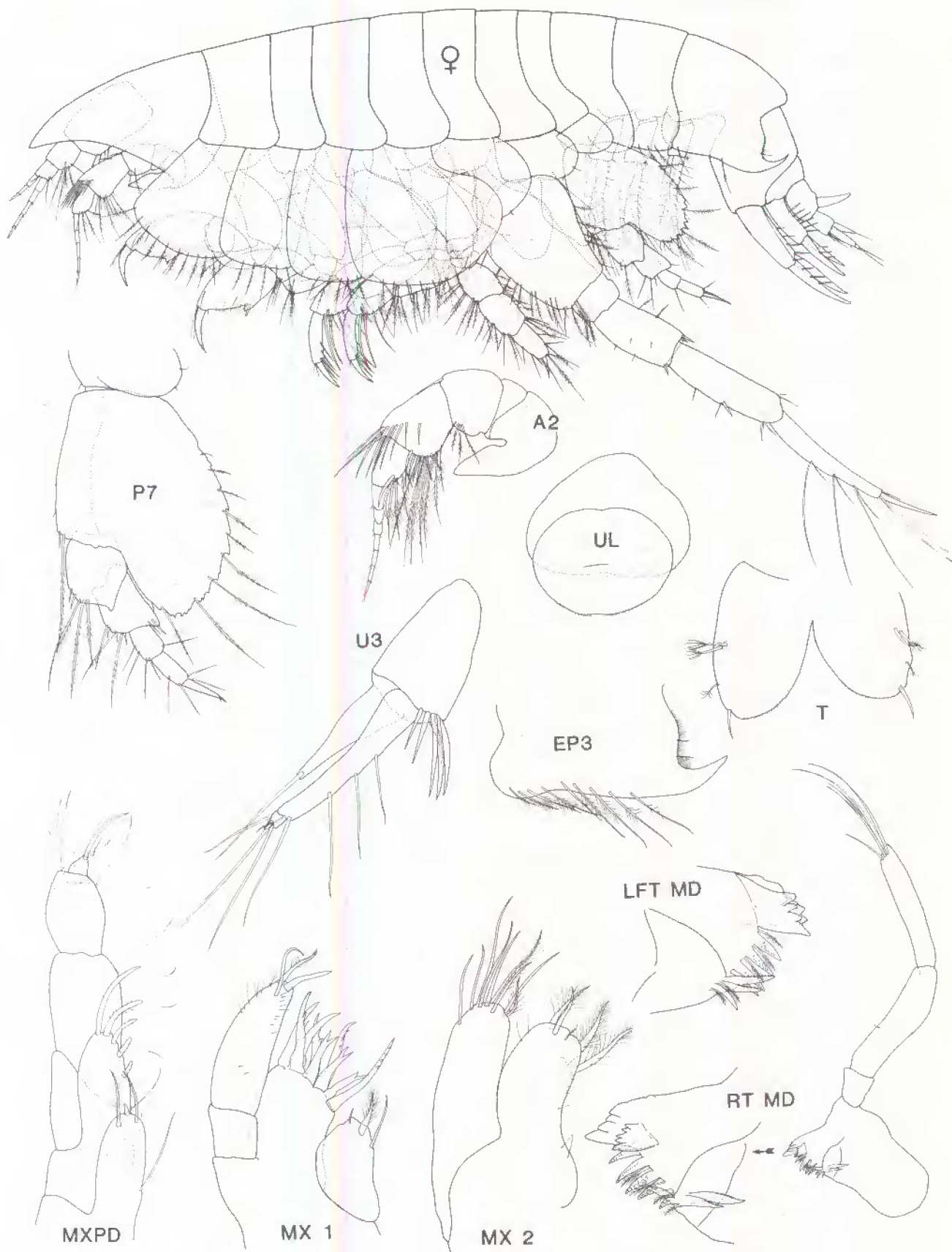
Mature Male: unknown.

Etymology: From the Latin root "*in - not + expectata*" - anticipated, not looked for. Since no other members of this genus are known from this region, the finding of this species here was unexpected.

Taxonomic Commentary: Material from the northern regions is clearly distinct from that identified as *P. sanpedroensis* by Barnard 1960, and even further remote from Chevreux's original *P. excavata*.

Distribution: Recorded from both inner and outer coasts of British Columbia, but to date not from localities north of Vancouver Island.

FIG. 35. *Pseudharpinia inexpectata*, new species.
FEMALE ov. (4.5 mm) HOLOTYPE.
(SEE PAGE 141 - OPPOSITE)



TAXONOMIC DISCUSSION

In this study, some 20 regional species of 5 phoxocephalid subfamilies other than Metharpiniinae have been recorded and described from the North American Pacific region, from the Bering Sea and Alaska to northern California. We conclude here by commenting on possible phyletic significance of some taxonomic findings, and on biogeographical relationships revealed by analysis of the distribution of component species.

A major phenomenon characterizing phoxocephalid amphipods is their high degree of sexual dimorphism, demonstrated by nearly all species within the five subfamilies treated here, and previously in the Metharpiniinae (Jarrett & Bousfield, 1994). In mature male instars, the diversity of sensory structures such as antennal calceoli seems especially remarkable. In anticipation of experimental confirmation, these organelles are believed to be sensitive to water-borne acoustical or mechanical vibrations (Lincoln & Hurley, 1981). If true, such a receptor apparatus may respond to vibrations emitted by females of the same species, and/or, in the case of carnivorous amphipods, the escape vibrations of prey organisms. Especially notable here are the large balloon- or paddle-shaped calceoli that occur facially on peduncular segment 5 of antenna 2 in males of the pontarpariniin genus *Mandibulophoxus*. These calceoli are easily overlooked because of their cryptic location on the medial facial surface of peduncular segment 5 of antenna 2, and because of the close similarity of body form and appendages between males and females in this genus. Similarly large calceoli may be present, cryptically, on antenna 2 of males not only in other species of this genus elsewhere (e.g. *M. uncirostratus*), but also in species of eyed (austral) genera of the subfamily (e.g. *Pontharpinia*, *Basuto*, and *Griffithsius*) in which antenna 2 of males has been described as similar to that of the female, not described, or is unknown (Griffiths, 1976a; Barnard & Drummond, 1978).

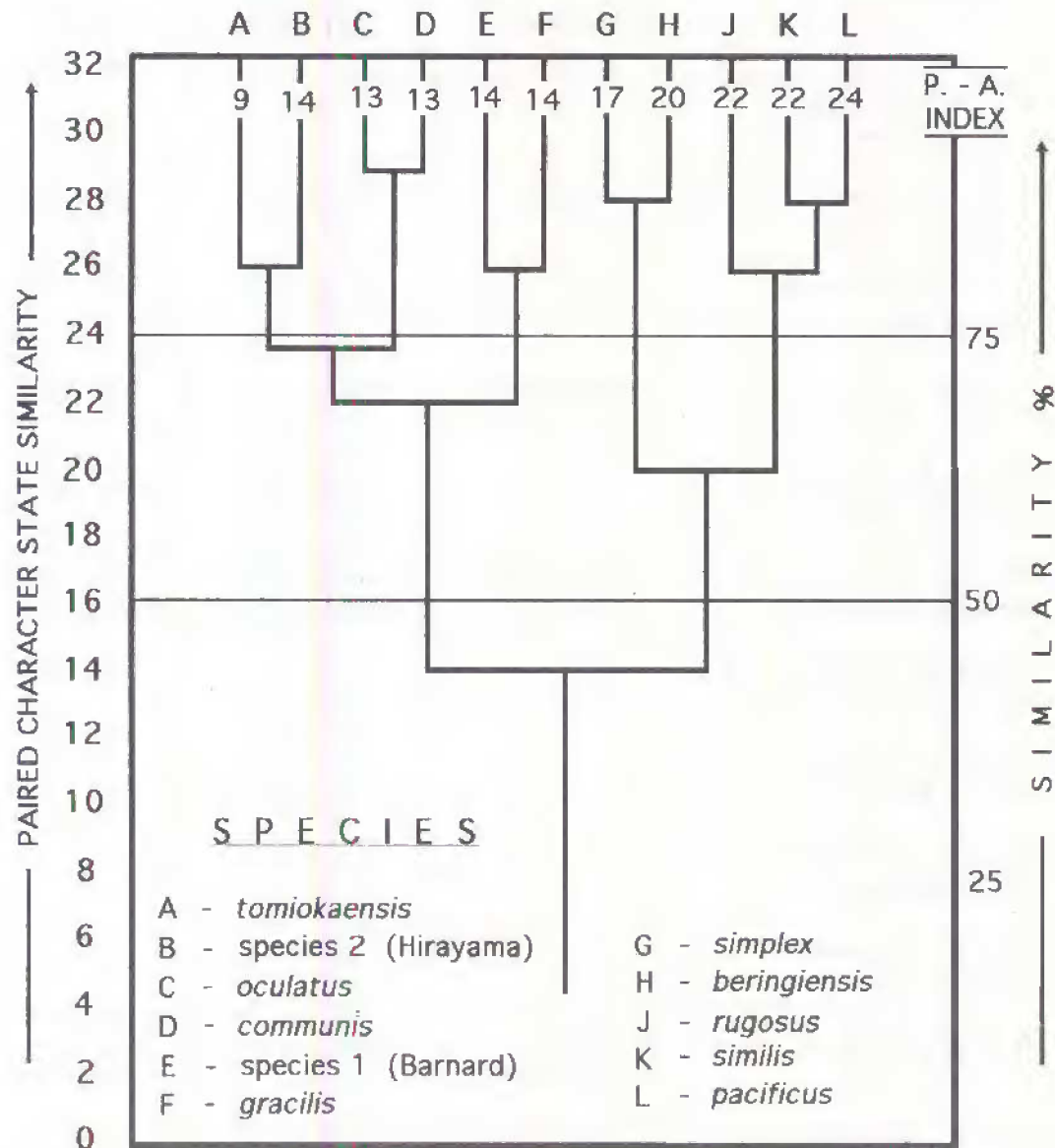
Superficial similarity of the antennae of males and females occurs widely in other sand-burrowing amphipods. The trend from long- to short-flagellate antennae, and loss of calceoli in males is evidenced in North American Atlantic species of *Amphiporeia* and *Bathyporeia* (Bathyporeiidae) and members of the more advanced Haustoriidae (Bousfield, 1973, 1990). As outlined in phyletic classifications of Bousfield (1982, 1983), the trend prevails in austral families within superfamily Phoxocephaloidea such as the Cheidae (Thurston, 1982), Condukiidae (Barnard & Karaman, 1991), and subgroups within family Urothoidae such as the phoxocephalopsids and zobrachoids (Barnard & Drummond, 1982). In the former (Bathyporeiidae), males still possess normal or slightly enlarged calceoli on anterior medial margins of the short flagella, but not on the peduncular segments. In the phyletically more advanced Haustoriidae, calceoli appear to have been totally lost. With respect to the presence of antennal calceoli, a plesiomorphic feature, all species of North American Pacific phoxid subfamilies are relatively primitive, and close to the subfamily ancestral morphotype.

An even greater range of morphological diversity was found here in the specialized spines and segmental modifications of peraeopod 7 of mature male instars. Pending observations on the actual mating behaviour of component species, these exoskeletal modifications form an apparatus believed to be used, in some manner, during actual copulation of male and female pairs, normally in the water column. The morphology of this apparatus, across a spectrum of phoxid subfamilies, has been outlined above (p. 73, fig. 1). Character states associated with this apparatus are believed to be significant in the phyletic classification of component species, but this premise awaits confirmation on a broader basis. The possibility of homoplasious similarity is real. Thus, as diagnosed above, the two subfamilies in which the clasping mechanism is on the anterior margin of segment 5, the Parharpariniinae and the Phoxocephalinae, are not very similar to each other in most other character states. As noted in figure 1 also, a similar modification of peraeopod 7 occurs in males of at least 3 of the 4 known genera of Pontoporeiidae, the type family of superfamily Pontoporeioidea that is phyletically gammaroidean rather than phoxocephaloidean.

Natural relationships among species groups can be tested more reliably by means of numerical taxonomic methodology. Here such study is handicapped by the relatively small number of species represented in most of the regional subfamilies and genera. Within subfamily Broilginae, however, the genus *Paraphoxus* proves to be well represented species-wise in the North Pacific region (see Table II) and is otherwise suitable for such analysis. A modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973) is employed here. It has been utilized previously in the study of morphological relationships in other amphipod groups (e.g. Conlan, 1983; Staude, 1986) and in other phoxocephalids (Jarrett and Bousfield, 1994).

The preparation of a phenogram of species similarities within the genus *Paraphoxus* (Fig. 36) is supported by analysis of pertinent characters and character states provided in Table I (p. 144). The phenogram "clusters out" two main subgroupings at less than 50% similarity, viz, a primitive *oculatus* group on the left (with P.-A. indices of 9-14), and an advanced *pacificus-rugosus* group on the right, (P.-A. indices of 17-24). The latter group is especially advanced in character states of maxilla 1 (outer plate apically 9-spinose), reduced spination of the uropod rami, and low number of spines on distal segments of the peraeopods. Within the *oculatus* subgroup, all species appear fairly closely related (above 75% similarity). Within the *pacificus* subgroup, we may identify a less advanced *simplex-beringiensis* complex (P.-A. indices of 17-20) and a more advanced *pacificus-similis* complex (P.-A. indices of 22-24). A cladistic analysis of these groups is likely to give similar results, particularly when males have been described for all component species, and their reproductively significant character states can be incorporated in the analysis. The biogeographical significance of these morphological relationships is noted below (p. 146).

FIG. 36. PHENOGRAM OF SPECIES OF *PARAPHOXUS*



BIOGEOGRAPHICAL DISCUSSION

This study analyses species distributions within five subfamilies of Phoxocephalidae that occur in littoral marine (shelf) waters of the North American Pacific region. The subregional occurrence of species and genera is provided in Table II. More than 30 species of these five subfamilies are listed here. Of the five subfamilies, four are pan-Pacific; only members of the Pontharpiniinae (*Mandibulophoxus*) do not occur on both sides of this northern ocean.

Treating the North Pacific fauna of 30+ listed species as a whole (pan-Pacific), 20 species have been identified from the region of study material, from the Bering Sea to northern California. The number is increased to 26 species if those of central and southern California are included. A similar

north-south species trend on the Asiatic coast, is indicated in existing records, mostly provided in the works of Gurjanova, 1951, 1977, 1980, etc.) and may be more broadly confirmed through the on-going studies of adjacent regional faunas, especially by Hirayama (1992). If we examine the totals for each subregion we find that high numbers (> 10 species) occur in zone 1 (Asiatic Pacific) and in zones 4, 5, 6 and 8 (North American Pacific). This feature contrasts with that of species of subfamily Metharpiniinae (Jarrett & Bousfield, 1994) wherein the numbers show an overall gradual increase from very few on the Asiatic and Bering Sea coasts to greatest species representation in southern California. The significance of these results with respect to present studies are tempered by limitations in geographical coverage and bathymetrical sampling at subtidal depths (>25 m.) where compo-

TABLE I. SPECIES OF *PARAPHOXUS*: CHARACTERS AND CHARACTER STATES

| CHARACTER | CHARACTER STATE VALUE | | |
|--|---------------------------------|---------------------------------|-----------------------------------|
| | Plesiomorphic 0 | Intermediate 1 | Apomorphic 2 |
| 1. Maxilla 1, outer plate, number of apical spines | 11 | 10 | 9 |
| 2. Antenna 2, peduncle 4, distal "fan" of spines | few, slender | medium | many, heavy |
| 3. Coxa 1, number of distal marginal setae | few, 3-6 | 7-9 | many, 10-14 |
| 4. Gnathopods 1 & 2, degree of similarity | subsimilar in size and form | differing in form | differing in both size and form |
| 5. Gnathopod 1, length of carpal free margin | long | intermediate | short, nearly cryptic |
| 6. Peraeopods 3 & 4; size of distal spine of segment 5 | small, < length segment 6 | intermediate length = segment 6 | large, strong, length > segment 6 |
| 7. Peraeopods 3 & 4; segment 6, no. distal spines | 3 | 1-2 | 0(1) |
| 8. Peraeopod 5, segment 6, no. front marginal spines | 3 | 2 | 1 |
| 9. Peraeopod 5, number of hind marginal setae | 2 | 1 | 0 |
| 10. Peraeopod 6, no. marginal spine/setal clusters | 4-6 | 7 - 10 | 11-15 |
| 11. Pleon plate 3, shape of hind corner | rounded margin convex | slightly produced | produced, lower margin straight |
| 12. Uropods 1 & 2, number of marginal ramal spines | many (2-3) | 1-2 | few (0-1) |
| 13. Uropod 3, strength of peduncular fan of spines | few (2-3) | 4-7 | many (8-10) |
| 14. Uropod 3, outer ramus, size terminal segment | short; 1/4-1/3 proximal segment | ~1/3 proximal segment | long, ~1/2 prox. segment |
| 15. Telson, L/W ratio of of each lobe | long, slender >2:1 | medium ~2:1 | short, broad <2:1 |

nent species are numerically most abundant, and ecologically dominant.

Regional endemism is expected to be high in sediment-dwelling amphipods, especially those that occur in shallow shelf waters (Jarrett & Bousfield, 1994). It is true that all five phoxid subfamilies and their 11 genera (of this study) are

well represented elsewhere, mostly in the southern hemisphere and some in the north Atlantic region. However, endemism of species in the North American Pacific region appears to be extraordinarily high. Thus, when the taxonomy of certain broad-ranging species such as "*Paraphoxus oculatus*" and "*Metaphoxus fultoni*" has been

TABLE III. DISTRIBUTION OF SELECTED PHOXID SUBFAMILIES, GENERA, AND SPECIES IN THE NORTH PACIFIC REGION

| TAXON | BIOGEOGRAPHICAL ZONE (legend on page 146) | | | | | | | |
|---------------------------------------|--|---|---|---|----|---|---|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| PONTOHARPINIINAE | | | | | | | | |
| 1. <i>Mandibulophus alaskensis</i> | | | X | X | X | | | |
| 2. <i>M. mayi</i> | | | | X | X | | | |
| 3. <i>M. gilesi</i> | | | | | X | X | X | x? |
| PARHARPINIINAE | | | | | | | | |
| 1. <i>Eyakia subuncigera</i> | X | | | | | | | |
| 2. <i>E. uncigera</i> | X | | | | | | | |
| 3. <i>E. calcarata</i> | X | | | | | | | |
| 4. <i>E. ochotica</i> | X | | | | | | | |
| 5. <i>Eyakia</i> sp. 1 (Barnard) | X | | | | | | | |
| 6. <i>Eyakia robusta</i> Holmes | | | | X | X | X | X | X |
| 7. <i>Eyakia</i> sp. 2 (Barnard) | | | | | | | | X |
| BROLGINAE | | | | | | | | |
| 1. <i>Eobrolgus pontarpioides</i> | X | | | | | | | |
| 2. <i>Eobrolgus chumashi</i> | | | X | X | X | X | X | X |
| 3. <i>Paraphoxus oculus</i> Sars | | | | | | | | |
| (Authentically North Atlantic) | | | | | | | | |
| 4. <i>P. tomiokaensis</i> | X | | | | | | | |
| 5. <i>P. species 2</i> | X | | | | | | | |
| 6. <i>P. communis</i> | | | | X | | | | |
| 7. <i>P. gracilis</i> | | | | | X | | | |
| 8. <i>Paraphoxus</i> species 1 (Bnd) | | | | | | | | X |
| 9. <i>P. simplex</i> Gurj. | X | ? | | | | | | |
| 10. <i>P. beringiensis</i> | | X | | | | | | |
| 11. <i>P. rugosus</i> | | X | | | | | | |
| 12. <i>P. pacificus</i> | | | X | X | x? | | | |
| 13. <i>P. similis</i> | | | | | X | | | |
| PHOXOCEPHALINAE | | | | | | | | |
| 1. <i>Cephalophoxoides prolixus</i> | X | | | | | | | |
| 2. <i>C. homilis</i> | | | | X | X | X | X | x? |
| 3. <i>Metaphoxus frequens</i> | | | X | X | X | X | X | X |
| 4. <i>Parametaphoxus asiaensis</i> | X | | | | | | | |
| 5. <i>P. quaylei</i> | | | | X | X | X | | |
| HARPINIINAE | | | | | | | | |
| 1. <i>Harpinia</i> spp. | X | X | | | | | | |
| 2. <i>Heterophoxus affinis</i> | | | X | X | X | X | X | X |
| 3. <i>H. conlanae</i> | | | X | X | X | X | | |
| 4. <i>H. ellisi</i> | | | | X | X | X | | |
| 5. <i>H. ellisi</i> var. | | | | X | X | | | |
| 6. <i>H. oculatus</i> | | | | | | | | X |
| 7. <i>Heterophoxus</i> spp. (S. Cal.) | | | | | | | | X |
| 8. <i>Harpiniopsis gurjanovae</i> | | X | | | | | | |
| 9. <i>H. fulgens</i> | | | | X | X | ? | ? | X |
| 10. <i>Pseudharpinia inexpectata</i> | | | | X | X | | | |

Legend for Biogeographical Zones of Table II.

I. Occurrence

- X - abundant in subregion (or presumed so)
- x - marginally occurring in subregion

II. Coastal SubRegions (Progression: Northwest to Southeast)

1. Japan and Western Pacific
2. Bering Sea and Aleutian Chain
3. Prince William Sound & southeastern Alaska (north of Dixon Entrance)
4. North-central coast of British Columbia and Queen Charlotte Islands
5. Southern British Columbia and Vancouver Island
6. Washington & Oregon
7. Northern and central California
8. Southern & Baja California

critically sorted out, none of the 20 study-region species is found to occur elsewhere. Of the ten genera represented in study collections here, all but one subgroup of *Paraphoxus* occur amphi-Pacifically in temperate-cold-temperate waters. They range northward only slightly into southeastern Alaska, and not at all into the Bering Sea region. Only in the deep-water Harpiniinae and one subgroup of Broilginae were member species found in the Bering Sea region or along the Alaska coast (subregions 2 & 3 of Table II, above). Species of all other genera show high regional endemicity or range southward into central and southern California. These southward-ranging groups appear to be matched to some extent on the Asiatic Pacific coast. Corresponding species pairs may be noted in at least four genera, viz., *Eyakia calcarata* and *Eyakia* spp. 1 & 2 of J. L. Barnard; *Eobrolgus pontarpioides* and *E. chumashi*, *Cephalophoxoides prolixus* and *C. homilus*; and *Parametaphoxus asiaensis* and *P. quaylei*. Within the genus *Paraphoxus*, we have noted (above) two distinct taxonomic subgroups which here show corresponding biogeographical differences. The primitive *oculatus* subgroup is cool-temperate and southward ranging, on both the North American and Asiatic Pacific coasts, and occurs elsewhere in warm temperate waters of the eastern Atlantic and Mediterranean region. By contrast, the advanced *pacificus-rugosus* taxonomic subgroup of *Paraphoxus* is endemic to cold-temperate Pacific waters and ranges north into the Bering Sea. A similar phenomenon may be detected elsewhere, within subfamily Metharpiniinae. Thus, only the genus *Grandifoxus* exhibits a similar cold-temperate N. American Pacific endemicity, whereas all four other genera of the subfamily range mainly southward into California.

The studies on the Metharpiniinae showed also that primitive members of shallow-water faunas tend to occur in colder northern biogeographic regions, and advanced members in warmer southern regions, with phylogenetically intermediate members mainly in the middle part of the range (Jarrett & Bousfield, 1994). This trend or pattern is the not clearly evidenced within the genera of subfamilies treated here,

probably because numbers of species are small, and the sampling was limited in scope. However, such a trend is suggested within the pontarpiin genus *Mandibulophoxus*. There the northern species, *M. alaskensis* is phylogenetically more primitive than the southern species *M. gilesi*. Also, in the *pacificus* subgroup within genus *Paraphoxus*, the most northern species, *P. simplex* has the lowest A.-P. index, whereas the most southerly species, *P. similis* and *P. pacificus* have highest P.-A. ratings, and are therefore most advanced.

Although the species numbers presented here are modest compared to those of other well-studied regions such as southeastern Australia (Barnard & Drummond, 1978), we may conclude that the faunistic affinities of at least four of these five subfamily groups is temperate and cold-temperate, and the principal range is southward in American Pacific coastal waters. We may conclude also that, in these same groups, endemicity at the genus level is moderate (three of 11 genera and one generic subgroup occur nowhere else in the North Pacific). However, at the species level, endemicity is extremely high since none of the North American Pacific species occurs elsewhere.

The results of this study suggests a possible relationship between phylogeny and biogeography of component subfamilies. Thus, subfamily Pontharpiniinae (whose genus is entirely North American endemic) matches distributionally subfamily Metharpiniinae in which only two species (of more than 30 subfamily members) have apparently penetrated to the Asiatic Pacific coast (Jarrett & Bousfield, 1994). According to that study (*loc. cit.*, Table I), families Metharpiniinae and Pontharpiniinae are the two most primitive regional subfamilies, with phyletic indices little above their close austral relative, the most primitive phoxid subfamily, Tipimeginae. The other four sub-families of this study are more strongly represented on the Asiatic Pacific coast, possibly because (in the case of the the most advanced Phoxocephalinae and Harpiniinae) the member species are better adapted to deep-water conditions. According to the standard vicariance model, the deeper-water groups presumably would be less affected by short-term (intra-epochal) geographical and climatic fluctuations, and show greater long-term stability, at all taxonomic levels, over a broader geographic area.

The general applicability of such theory appears to be validated by the high degree of endemic speciation within the two primitive North American Pacific phoxid sub-families. These also contain the highest percentage of member species that occur intertidally or in shallow-water habitats, above the summer thermocline, and subject to widest annual thermal fluctuations. It would seem therefore, that the North American Pacific phoxocephalid fauna retains a major component of phylogenetically primitive or relict groups, early derived from southern austral regions, along with more modern groups that have spread from the edaphically rigorous shallows into physically more stable but less nutrient-rich environments of fiords and deeper off-shore waters.

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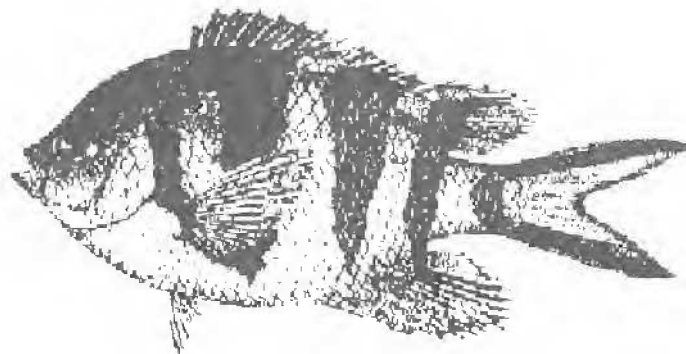


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